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Artículo

The forgotten habitats in conservation: early successional vegetation
Los hábitats olvidados en conservación: la vegetación de estados sucesionales tempranos

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Abstract
Conservation efforts in terrestrial environments have focused on preserving patches of natural habitats and restoring disturbed habitats, with the main goal of transforming them into forests or habitats that resemble the original conditions. This approach tends to overlook the importance of conserving early successional vegetation (e.g., riverside vegetation, natural regeneration, young secondary forests), which often includes a large number of species (e.g., plants and animals) associated with or restricted to these habitats. In this paper we want to bring to attention the importance of preserving early successional vegetation, and to encourage scientists to investigate, e.g., the diversity, distribution, and species interactions occurring in these habitats. To address these goals, we focus on two main objectives: (1) to identify the common types of early successional vegetation in the Costa Rican Central Valley; and (2) to use some case studies to draw attention to the importance that such areas have as reservoirs of a large portion of the diversity unique to early successional stages. We first include an example to show the diversity of plants in small forest patches immersed in a large urbanized area. We provide general information on the insects that occur in early successional vegetation in urban areas, and in further detail examples of butterflies. Additionally, we provide examples of birds and mammals that are restricted to early successional vegetation, and how the reduction of this vegetation type affects species conservation. Finally, we encourage scientists to investigate these early successional habitats, particularly those species exclusive to early successional stages. Special attention should be paid to endemic species and those with a restricted distribution. Information of this type will make conservation of the diversity contained in these habitats possible.
Key words: thickets; mammals; birds; insects.

Resumen
Los esfuerzos de conservación en ambientes terrestres se han centrado principalmente en la preservación de ambientes naturales y la restauración de diferentes hábitats, con la meta principal de transformar estos ambientes en bosques maduros o hábitats que asemejen las condiciones originales. Este enfoque tiende a pasar por alto la importancia de conservar la vegetación de estados de regeneración temprana (e.g., vegetación riparia, regeneración natural, bosque secundario joven), la cual incluye un gran número de especies (e.g., plantas y animales) asociadas o restringidas a estos hábitats. Con este artículo queremos llamar la atención sobre la importancia de preservar áreas cubiertas con vegetación de sucesión temprana, e instar a científicos y naturalistas a investigar, e.g., la diversidad, distribución, e interacciones entre las especies presentes en estos ambientes. Para apoyar esta meta, nos enfocamos en dos objetivos principales: (1) identificar los tipos más comunes de vegetación

pionera en el Valle Central de Costa Rica; y (2) utilizar algunos casos de estudio para llamar la atención sobre la importancia que tales áreas tienen como reservorio de gran parte de la diversidad, mucha de la cual es única de los estados de sucesión temprana. Primero se incluye un ejemplo particular en el cual se muestra la diversidad de plantas en pequeños fragmentos de bosque y matorral inmersos en una gran área urbanizada. Después se presenta una revisión general de los insectos que habitan en la vegetación de sucesión temprana en áreas urbanas, para luego discutir en mayor detalle ejemplos de mariposas. Además, proporcionamos ejemplos de especies de aves y mamíferos que están restringidos a vegetación de sucesión temprana, y cómo la reducción de este ambiente afecta su conservación. Finalmente, instamos a los científicos de diferentes áreas a investigar los diversos procesos ecológicos e interacciones biológicas inherentes a los estados de regeneración temprana. Especial atención requieren aquellas especies exclusivas o endémicas de estos ambientes. Sin esta información es imposible conservar la diversidad de estos hábitats.
Palabras clave: matorrales; mamíferos; aves; insectos.

Introduction

For nearly two centuries the great diversity and exuberance of tropical forests have attracted the attention of naturalists and scientists (Gentry, 1990; Kricher, 1999; Forsyth & Miyata, 2011). The pristine ecosystems and communities in these forests have been the focus of numerous investigations. Particular attention has been paid to understanding the causes of the large diversity and complex interactions among tree species and animal communities that inhabit tropical forests (Eisenberg, 1990; Karr, Robinson, Blake, & Bierregaard, 1990; Whittaker, Willis, & Field, 2001; Ghazoul, 2002; Wright, 2002; Schulze et al., 2004). However, immersed within the matrix of huge trees are some naturally disturbed sites (e.g., forest gaps, thickets, or landslides), which include a different set of plant and animal species with different adaptations, life history traits, and ecological requirements (Connell, 1989; Brokaw & Busing, 2000).

Early successional vegetation like that in forest gaps is an example of an ephemeral habitat produced randomly in the forest by intermediate disturbances (Lorimer, Frelich, & Nordheim, 1988; Young, & Hubbell, 1991). Once a gap is produced (e.g., tree fall or landslide), a gradient of environmental variables occurs from the edge to its center. These altered environments also produce an ecological gradient that is occupied by a mixture of plant and animal species adapted to these ephemeral habitats (Connell, 1989; Schupp, Howe, Augspurger, & Levey, 1989; Kursar & Coley, 1999).

Some life-history traits are shared by the species adapted to these relatively ephemeral habitats. Plants adapted to such habitats have a reproductive r-strategy and high dispersal capability that allow them to colonize and reproduce in ephemeral and randomly distributed environments (Wilson & Bossert, 1971). Most of these plants are therefore short-lived with high investment in reproduction and little in maintenance. Animals and other organisms have been less studied, but it is known that in large mature forests some bird and insect species are found only in early successional vegetation such as forest gaps but not in the surrounding mature forest (Levey, 1988; Schnitzer & Carson, 2001). Animals and plants in forest gaps and similar early successional vegetation are thus expected to share some life history traits (e.g., high reproductive rate and/or high dispersal capability) to cope with the ephemeral conditions and often random distribution of these areas.

In pristine environments, early successional habitats are relatively scarce and only cover a small area of the total environment, but human processes have changed their dynamics and characteristics. First, human destruction of pristine forests has, in some cases, artificially created extensive areas that represent different natural ecological successional phases that occur in pristine conditions. For example, large areas previously covered with pristine forests are now covered with thickets or second growth vegetation (Cardoso Da Silva & Bates, 2002; Joyce, 2006). Second, the rapid expansion of urbanization is eliminating the second growth vegetation, with no concern for the diversity found in such habitats (Biamonte, Sandoval, Chacón, & Barrantes, 2011; Forman, 2014; Johnson & Swan, 2014). It is understandable that for their rich biodiversity and size of trees, pristine or mature forests have become a main focus of conservation. However, early successional vegetation (e.g., herbaceous areas and second growth forest patches), deserves more attention for at least two reasons. First, this vegetation is a reservoir for a considerable part of our biodiversity, which is uncommon in pristine environments. Second, this is the only vegetation that partially ameliorates the drastic changes caused by urbanization, for example by reducing the heat in large cities and stabilizing soil that prevents landslides (Rosenfeld, Akbari, Romm, & Pomerantz, 1998; Onishi, Cao, Ito, Shi, & Imura, 2010; Forman, 2014). The objective of this paper is to use some Costa Rican case studies to draw attention to the importance that early successional vegetation and second growth forest patches have as reservoirs of biodiversity. The case studies included in this paper are based on soft rather than hard data, which reflects the relative lack of research interest in human altered environments, particularly in or near urban areas.

Definition of early successional vegetation

We included under early successional vegetation several types of altered and second growth habitats.

Riverside vegetation: this category includes vegetation in different successional stages maintained by flooding and landslides that impact the streams and rivers' edge vegetation mainly during the rainy season in different forest types.

Altered land-cover: this is a general category that includes forest edges, abandoned grasslands, or open fields with tall, dense grasses and low overgrown tangles of shrubs and vines (Fig. 1).

Young secondary forests: it includes areas with dense herbaceous and bushy understory, with abundant small trees, and some sparse remnant old trees. Under some conditions the formation or expansion of these habitats may be caused by human disturbance (Fig. 1).

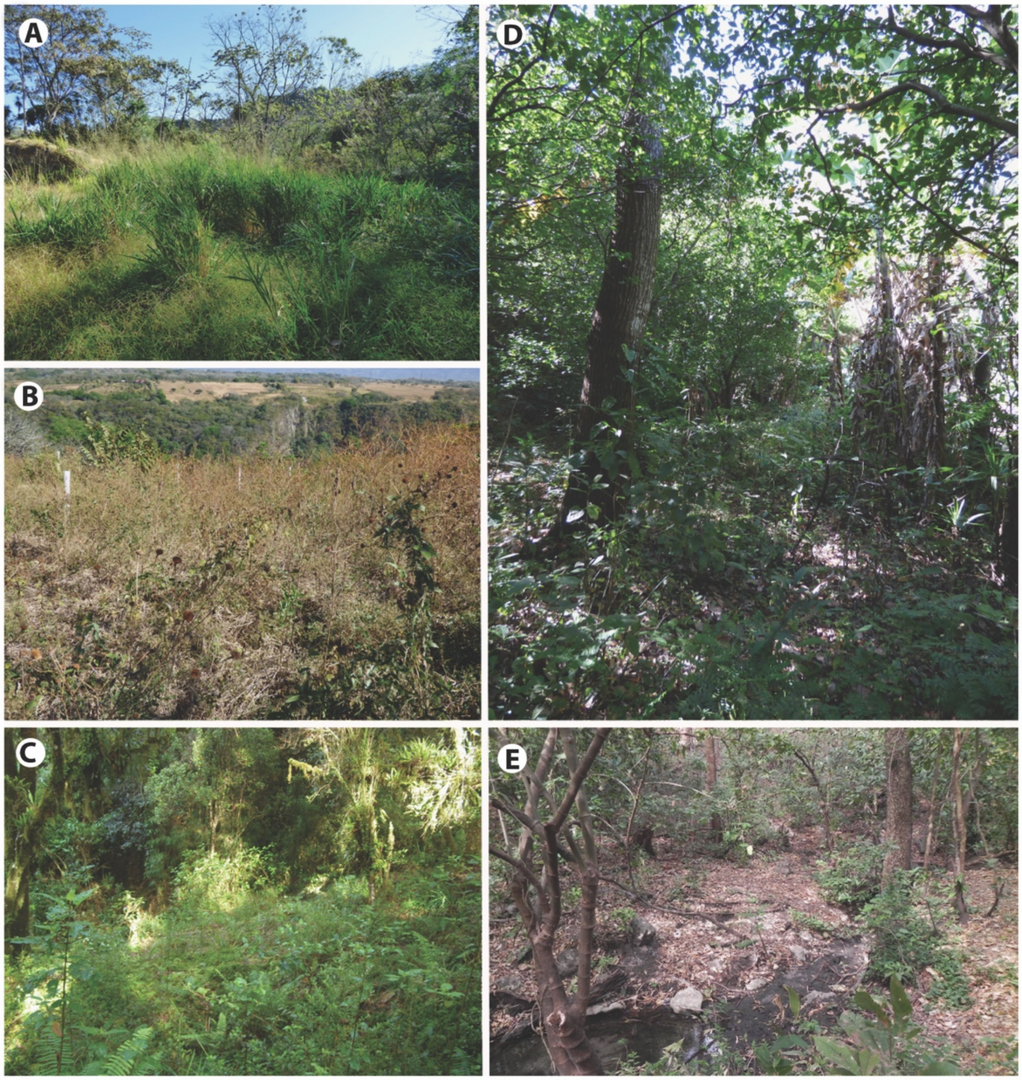

Fig. 1. Different types of early successional vegetation. **a-** Grassy vegetation with some dispersed, sun tolerant trees; **b-** early successional herbaceous vegetation; **c-** high montane forest edge; **d-** second growth premontane forest; **d-** second growth dry forest. (a, b, d: southwestern Central Valley; c: Talamanca mountain range; d: Palo Verde National Park).

Case studies

We selected five case studies of Costa Rican organisms to respond to the objective of this study. The case studies include vegetation, insects, butterflies, birds, and mammals that inhabit urban habitats and/or habitats that have been drastically modified by changes in land-use. The information included in each case study varies largely, which, in general, indicates the little information on most aspects of the ecology of the species inhabiting urban habitats. The first two cases (vegetation and insects) focus on the diversity and occurrence of species in small vegetation areas (i.e., small second growth forest patches and small patches of herbs and bushes, respectively) immersed in a large urban matrix. The third case includes several butterfly species to exemplify the use of second growth vegetation in or around the large Costa Rican cites, though some of the species included use similar vegetation over a more extended altitudinal and geographical distribution. The last two study cases focus on particular species, specialized on second growth vegetation to show the importance of this type of vegetation for species that require this environment to maintain their populations.

Case study 1-Vegetation of urban green areas: The Costa Rican Central Valley includes the four largest cities and the greatest human population in the country. Immersed within this large, densely populated area, are some small green areas that serve as reservoirs of plant and other organisms' diversity. Two examples are the Leonelo Oviedo Ecological Reserve (9º56'15''N & 84º03'00'W; Nishida, Nakamura, & Morales, 2009) and the Orozco Botanical Garden (9°56'05.80" N & 84°03'07.39" W; Amador, 2007), both on the campus of the University of Costa Rica (UCR, Montes de Oca, San José, 1 205 - 1 213 m.a.s.l.). These green oases protect hundreds of plant species with different habits (e.g., trees, vines, herbs), which are used for food, nesting, and refuge by a large number of insect, bird, and mammal species that still inhabit this part of the Central Valley.

The Leonelo Oviedo Preserve (ca. 1.93 ha) is a secondary forest recovered after eliminating a coffee plantation in the 1960´s, now with some management practices that include reforestation with native species, and removal of some invasive plants. This is the habitat of ca. 250 vascular plants species (Nishida et al., 2009; COM unpubl. data), including 36 (18 %) tree species that are native to this portion of the Central Valley, thereby representing a remnant of the original forests that covered most of this region more than 500 years ago. During the last decade two orchid species previously unknown for the Central Valley were collected along the Quebrada Negritos stream that runs along the edge of this preserve: *Catasetum maculatum* Kunth, a small, immature plant fallen from a *Cedrela odorata* L. tree, and the tiny *Trizeuxis falcata* Lindl. (M. Bonilla s. n., USJ-100753) flowering on a riparian tree.

The Orozco Garden (ca. 0.45 ha) was established in the early 1930's. This is not a classical botanical garden with European design; instead, it represents an intermediate physiognomy between an arboretum and a regenerated forest, with native and introduced species. This area protects (at the beginning of 2018) 950 species (COM, unpubl. data). This extraordinarily species rich small area, with only a quarter of hectare, is among the most species-rich sites in the whole world. It contains more species than the richest tropical rain forest ever registered (942 species/ha in Ecuador; Balslev, Valencia, Paz y Miño, Christensen, & Nielsen, 1998; Wilson, Peet, Dengler, & Pärtel, 2012).

During the last two decades some species of herbs and shrubs that have gradually been extirpated from other ruderal sites in the central and eastern part of the Central Valley were detected in one or both of these forest patches. The presence of these species in these forest patches is likely due to the germination of seeds that remained dormant in the soil for years or decades after elimination of the reproductive individuals, or transportation by abiotic agents or animals [e.g., *Inga* spp., *Persea caerulea* (Ruiz & Pav.) Mez, *Sapium macrocarpum* Müll. Arg., *Senna papillosa* (Britton & Rose) H.S. Irwin & Barneby, *Stemmadenia litoralis* (Kunth) L. Allorge, and *Trichilia havanensis* Jacq.]. In other cases, the protection of one or more individuals of some species may have made propagation of seeds possible [e.g., some Asteraceous shrubs and small trees spreading by wind like *Montanoa hibiscifolia* Benth., *Podachaenium eminens* (Lag.) Sch. Bip., *Vernonia patens* Kunth, and *V. triflosculosa* Kunth].

At least 50 native and introduced plant species (COM, unpubl. data) have been extirpated in the past 20 years (1998-2018) outside these two protected patches. Because this pattern has been similar or worse in the rest of the valley outside the campus during the same period, it is likely that several hundreds of plant species became lost in the whole Central Valley [e.g., *Amaranthus spinosus* L., *Calliandra calothyrsus* Meisn., *Chenopodium ambrosioides* L., *Frangula pendula* A. Pool, *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult., *Psychotria horizontalis* Sw., *Rivina humilis* L., *Staphylea occidentalis* Sw., and *Tournefortia glabra* L.], and this would correlate strongly and sadly with a well-documented reduction of avifauna in this region during the last 50 years (1968-2018: Stiles, 1990; Biamonte et al., 2011).

With a little effort, part of the vegetation that has rapidly been lost during the last decades could be recovered. Two cypress trees (*Cupressus lusitanica* Mill.) and one species of grass that occupied a small area of only ca. 45 m^2 (northeast side of the Biology building, UCR) were removed. A few species [e.g., *Calathea crotalifera* S. Watson, *Clidemia* sp., *Erythrina berteroana* Urb., *Piper aduncum* L., *Sapium macrocarpum* Müll. Arg., and *Senna septemtrionalis* (Viv.) H.S. Irwin & Barneby)] were planted and then regeneration was allowed to progress. Over the next five years 68 species, 64 genera and 32 families of vascular plant species have been recorded, most of them herbs, shrubs and pioneer trees, with 80 % being native species (COM unpubl. data). Regeneration in this small area likely occurred mainly through germination of seeds in the soil seed bank and those dispersed by animals, wind and other factors [e.g. the bushes *Hyptis suaveolens* (L. Poit.), *Solanum rudepannum* Dunal, and

Vernonia sp.]. Paralleling plant regeneration, a large number of insects and spiders have also occupied this small area and some bird species have become frequent visitors for feeding and roosting.

Case study 2-General information on insects in urban areas: This case study provides information on the diversity of different groups of insects that remain in small patches of second growth vegetation in urban environments. When compared to less altered areas, early successional vegetation in urban areas generally have fewer species of native insects and an increased abundance of invasive species (New, 2015). Nonetheless, because insects are so poorly studied, urban areas contain a surprising number of undescribed species; for example, 43 new species of *Megaselia* flies (Phoridae) were recently discovered in Los Angeles, California (Hartop, Brown, & Disney, 2016). Results from urban areas in tropical countries will probably be even more astounding and this unknown biodiversity should be conserved, even as we attempt to control a small minority of species that behave as pests.

Conservation of urban insect biodiversity is very difficult without environmental education, which should begin with the dictum that insects comprise a very large number of species, but just small minorities are injurious. For example, in Costa Rica there are nearly 200 species of cockroaches but only about a dozen invade our homes. There are about 900 species of ants but probably fewer than 20 are sometimes problematic. The African honey bee is just one of the nearly 700 species of bees. A large number of species are directly beneficial, for example by pollinating backyard fruit trees (Hedström, 1988), reducing populations of plant pests (Fenoglio, Videla, Salvo, & Valladares, 2013), and removing dog feces (Wallace & Richardson, 2005; Ramírez-Restrepo & Halffter, 2016). Insects also serve as food resource for many insectivorous birds (Tallamy, 2012).

Native plants in early successional vegetation nearly always harbor a greater diversity of insects than do introduced plants (Perre, Loyola, Lewinsohn, & Almeida-Neto, 2011). An obvious example is the differences between the introduced *Ficus benjamina* L. and *F. microcarpa* L. f. (Moraceae), common in secondary understory, versus any of the native fig species. Among the very few insects encountered on these introduced fig trees are an introduced species of gall-forming thrips (Thysanoptera) and an introduced bug (Anthocoridae) that preys on the thrips (Tavares, Torres, Silva-Torres, & Vacari, 2013). In contrast, native figs such as *F. costaricana* (Liebm.) Miq. harbor a rich diversity of insects, including at least a dozen species just in the fruits, plus an additional, incompletely documented diversity on other parts of the tree (PH, unpubl. data).

In early successional vegetation floral resources may be limited, yet pollen and nectar are necessary for several insect species (Winfree, Bartomeus, & Cariveau, 2011). For example, *Acnistus arborescens* (L.) Schltdl. (Solanaceae) is commonly viewed as a weed, but twelve native bee species have been observed visiting its flowers on the University of Costa Rica campus over a period of two months (Valverde & Leandro, pers. comm.). Other plants such as *Lantana camara* L. (Verbenaceae) attract various species of butterflies (Krenn, 2008). In addition, it should be mentioned that providing overripe fruit in the back yard instead of the garbage, supply butterflies with food resources that could help to maintain the diversity of this group in urban environments.

Early successional vegetation also provides nesting sites for bees and solitary wasps. These bees and wasps are not aggressive and generally do not sting (unless they are captured by hand). “Bee hotels”, such as boxes for stingless bees (Sommeijer, 1999) and bundles of hollow bamboo or wooden blocks with holes for solitary bees (Mader, Spivak, & Evans, 2010), provide nesting sites for a diversity of species in early successional vegetation. For example, bamboo nests placed on the University of Costa Rica campus for six months yielded *Megachile* bees and two species of wasps that prey on cockroaches, *Ampulex* sp. (Ampulicidae) and *Podium denticulatum* (Sphecidae) (Mora & Hanson, unpubl. data). There is an obvious desire on the part of home owners and gardeners to remove dead branches from shrubs and trees, but these overlooked habitations provide valuable nesting sites; for example, *Ceratina* bees (Apidae: Xylocopinae) have been found nesting in dead twigs of *Lantana camara* (PH, unpubl. data). Dead wood in early successional vegetation is an extremely important habitat for numerous beetles and other insects (Seibold et al., 2015). A Malaise trap set up next to a pile of dead wood in a back yard in Santo Domingo, Heredia province, Costa Rica (9°59’6.5” N & 84°5’35.6” W) yielded many insects normally found in primary forests, for example the relatively rare hymenopteran family Orussidae (PH, unpubl. data).

Case study 3-Butterflies: This case study provides examples of Costa Rican butterflies that inhabit small patches of early successional vegetation and gardens within and around the large cities, and other altered habitats in the country. Early successional vegetation shows a predominance of shade intolerant, annual and perennial herbs and shrubs (Swanson et al., 2011), and butterflies are common inhabitants of these early successional sites. Successional vegetation offers abundant nectar for butterflies to feed upon, and host plants for the development of butterfly larvae. In addition, the intense and long periods of solar radiation attract a large number of butterfly species to early successional vegetation, since their activity and often their courtship behavior depend on high temperatures.

Costa Rica has a large diversity of butterflies, with approximately 1 541 described diurnal species in six families: Hesperiidae, Papilionidae, Pieridae, Riodinidae, Lycaenidae, and Nymphalidae (Chacón & Montero, 2007). This represents 9.5 % of the global butterfly species. The breeding habitats of butterflies are tightly linked to their host plants, though feeding sources and daily or seasonal movements are also important to define their breeding habitats.

Following are some examples of butterflies that mainly or exclusively inhabit early successional vegetation. Females of *Battus polydamas* (Papilionidae), *Phoebis sennae* and *Aphrissa statira* (Pieridae) oviposit on plant species which generally grow in secondary forests such as *Aristolochia* spp. (Aristolochiaceae) and *Senna* spp. (Fabaceae), respectively. Both sexes emerge in this habitat and then fly to other early successional areas to feed on nectar and reproduce. In other cases, butterfly species find both their host plants and nectar plants in the same areas of early successional vegetation. That is the case of *Eurema daira* (Pieridae), *Anartia fatima* and three Costa Rican *Danaus* species (Nymphalidae).

Poaceae (grasses) is one of the most species-rich plant families in early successional vegetation (e.g., open areas, cattle pastures, abandoned fields). Two common grass species at low and mid elevation (Márquez, Fariñas, Briceño, & Rada, 2004; Dagnachew et al. 2014), the native *Panicum trichoides* Sw. and the introduced African *Eleusine indica* (L.) Gaertn. (Nilsson, Sánchez-Vindas, & Manfredi, 2005) are host plants for several butterfly species: *Taygetis laches, Cissia pompilia, C. confusa, C. pseudoconfusa, Magneuptychia libye* and *Pareuptychia ocirrhoe* (Nymphalidae) (DeVries, 1987). Adults of these species feed on decomposing material (e.g., fungi, fruits, branches, flowers, animal bodies), which is a common resource in early successional vegetation.

Three Costa Rican monarch species (*Danaus plexippus, D. eresimus* and *D. gilippus*) (Nymphalidae) are common inhabitants of open areas from sea level up to 2 000 m. These butterflies fly over these habitats searching for *Asclepias curassavica* L. (Asclepiadaceae), a common weed in early successional vegetation (Vega, 2010), to oviposit and feed on its nectar. Other common plants in these habitats are also used by *Danaus* spp. to obtain pyrrolizidine alkaloids (e.g., *Ageratum conyzoides* L., Asteraceae) as a defense against predators (Edgar, Cockrum, & Frahn, 1976), and to exploit their nectar (e.g., *Cosmos bipinnatus* Cav. and *C. sulphureus* Cav., Asteraceae).

Whites (Pieridae) are very common butterflies in early successional habitats. *Ascia monuste* and *Leptophobia aripa* fly just above the herbaceous layer in open areas searching for flowers of *Impatiens* spp. (Balsaminaceae) and a wide variety of herbaceous and shrubby Asteraceae (DeVries, 1987), and *Stachytarpheta* spp. (Verbenaceae). *Ascia monuste* lays eggs on *Lepidium virginicum* L. (Brassicaceae) and *Tropaeolum majus* L., while *Leptophobia aripa* lays eggs on *Tropaeolum moritzianum* Klotzsch (Tropaeolaceae) (DeVries, 1987) and *Lepidium virginicum* (RM-H, unpubl. data), which grow in early successional habitats. Similarly, *Cyclospermum leptophyllum* (Pers.) Sprague (Apiaceae) and *Lantana urticifolia* Mill. (Verbenaceae) which grow along roadsides and open areas are respectively the host and feeding plants of the swallowtail *Papilio polyxenes* (Papilionidae) (Nilsson et al., 2005).

Some butterfly species that naturally inhabit pristine environments occasionally occur in altered environments. This is the case of *Cyllopsis philodice, Eretris hulda,* and *Pronophila timanthes* (Satyrinae). These species were originally restricted to natural *Chusquea* spp. (Poaceae) thickets, where they lay their eggs and stay near *Chusquea* thickets to feed upon decomposing organic matter such as fungi, excrement, fruits, or stalks. With the cultivation of ornamental bamboos *Bambusa vulgaris* Schrad. ex J. C. Wendl., *Guadua angustifolia* Kunth, and *Phyllostachys aurea* Carrière ex Rivière & C. Rivière, some of these butterfly species have adapted to use this resource in urban areas. A summary of some of the Costa Rican butterfly species inhabiting early successional is provided in Table 1.

TABLE 1
Butterfly species that inhabit early successional vegetation in Costa Rica, habitat type, and occurrence and resource used by each species

Species	Thicket specific	Early succession	Early succession and secondary forest	Occurrence and resource used
Papilio polyxenes stabilis		X		Open areas host plants
Battus p. polydamas			X	Open areas host plants
Phoebis argante			X	Favorite flowers
Phoebis sennae			X	Favorite flowers
Aphrissa statira			X	Favorite flowers
Pyrisitia proterpia		X		Open areas host plants
Eurema daira		X		Open areas host plants
Anartia fatima		X		Open areas host plants
Anartia jatrophae		X		Open areas host plants
Jononia evarete		X		Open areas host plants
Euptoieta hegesia		X		Open areas host plants
Anthanassa drucilla		X		Open areas host plants
Anthanassa ardys		X		Open areas host plants
Anthanassa frisia		X		Open areas host plants
Microtia elva		X		Open areas host plants
Danaus plexippus		X		Open areas host plants
Danaus gilippus		X		Open areas host plants
Danaus eresimus		X		Open areas host plants
Cyllopsis philodice	X			Host plant dependent
Cyllopsis argentella	X			
Hermeuptychia hermes	X			Open areas host plants

Oexoschistus tauropolis	X			Host plant dependent
Eretris hulda	X			Host plant dependent
Eretris suzannae	X			Host plant dependent
Pronophila timanthes	X			Host plant dependent
Calephelis spp.		X		Favorite flowers
Cyanophrys herodotus		X		Host plant dependent

Case study 4-Birds: Of the 920-bird species in Costa Rica (Sandoval & Sánchez, 2017), 88 are specialists on early successional vegetation in different parts of the country (Table 2). Nine of these species are migratory from North America and use this vegetation as the main wintering habitat and 79 are residents in Costa Rica (one species has migratory and resident populations; Table 2). Of the 79-resident species, 15 are endemic to the country (Table 2). In addition to the specialist species, several other species inhabit or use this habitat, especially around cities where the majority of natural vegetation has been eliminated and transformed into urban development (Karr, 1976; Biamonte et al., 2011).

TABLE 2
Bird species that inhabit early successional vegetation in Costa Rica, with information on the species status in the country

Taxa*	English name	Status
TINAMIFORMES		
Tinamidae (5)		
Crypturellus soui	Little Tinamou	Resident
Crypturellus cinnamomeus	Thicket Tinamou	Resident
GALLIFORMES		
Cracidae (5)		
Ortalis vetula	Plain Chachalaca	Resident
Ortalis cinereiceps	Gray-headed Chachalaca	Resident
Odontophoridae (8)		
Dendrortyx leucophrys	Buffy-crowned Wood-Partridge	Resident
Odontophorus guttatus	Spotted Wood-Quail	Resident
COLUMBIFORMES		
Columbidae (25)		
Leptotila verreauxi	White-tipped Dove	Resident
Leptotila cassinii	Gray-chested Dove	Resident

Leptotila plumbeiceps	Gray-headed Dove	Resident
GRUIFORMES		
Rallidae (17)		
PASSERIFORMES		
Thamnophilidae (22)		
Cymbilaimus lineatus	Fasciated Antshrike	Resident
Taraba major	Great Antshrike	Resident
Thamnophilus doliatus	Barred Antshrike	Resident
Thamnophilus bridgesi	Black-hooded Antshrike	Resident (endemic)
Thamnophilus atrinucha	Black-crowned Antshrike	Resident
Cercomacroides tyrannina	Dusky Antbird	Resident
Gymnocichla nudiceps	Bare-crowned Antbird	Resident
Grallariidae (4)		
Hylopezus perspicillatus	Streak-chested Antpitta	Resident
Hylopezus dives	Thicket Antpitta	Resident
Grallaricula flavirostris	Ochre-breasted Antpitta	Resident
Rhinocryptidae (1)		
Scytalopus argentifrons	Silvery-fronted Tapaculo	Resident (endemic)
Furnariidae (34)		
Clibanornis rubiginosus	Ruddy Foliage-gleaner	Resident
Thripadectes rufobrunneus	Streak-breasted Treehunter	Resident (endemic)
Automolus ochrolaemus	Buff-throated Foliage-gleaner	Resident
Synallaxis albescens	Pale-breasted Spinetail	Resident
Synallaxis brachyura	Slaty Spinetail	Resident
Tyrannidae (82)		
Capsiempis flaveola	Yellow Tyrannulet	Resident
Mionectes oleagineus	Ochre-bellied Flycatcher	Resident
Sublegatus arenarum	Northern Scrub-Flycatcher	Resident
Pipridae (8)		
Manacus candei	White-collared Manakin	Resident
Manacus aurantiacus	Orange-collared Manakin	Resident (endemic)
Vireonidae (16)		
Cyclarhis gujanensis	Rufous-browed Peppershrike	Resident
Hylophilus flavipes	Scrub Greenlet	Resident
Troglodytidae (24)		

Pheugopedius atrogularis	Black-throated Wren	Resident (endemic)
Pheugopedius rutilus	Rufous-breasted Wren	Resident
Pheugopedius maculipectus	Spot-breasted Wren	Resident
Pheugopedius fasciatoventris	Black-bellied Wren	Resident
Thryophilus rufalbus	Rufous-and-white Wren	Resident
Thryophilus pleurostictus	Banded Wren	Resident
Cantorchilus thoracicus	Stripe-breasted Wren	Resident
Cantorchilus modestus	Cabanis's Wren	Resident
Cantorchilus zeledoni	Canebrake Wren	Resident (endemic)
Cantorchilus elutus	Isthmian Wren	Resident
Cantorchilus nigricapillus	Bay Wren	Resident
Cantorchilus semibadius	Riverside Wren	Resident (endemic)
Polioptilidae (4)		
Ramphocaenus melanurus	Long-billed Gnatwren	Resident
Turdidae (15)		
Catharus aurantiirostris	Orange-billed Nightingale-Thrush	Resident
Catharus fuscater	Slaty-backed Nightingale-Thrush	Resident
Catharus frantzii	Ruddy-capped Nightingale-Thrush	Resident
Catharus mexicanus	Black-headed Nightingale-Thrush	Resident
Rhodinocichlidae (1)		
Rhodinocichla rosea	Rosy Thrush-Tanager	Resident
Passerellidae (25)		
Pselliophorus tibialis	Yellow-thighed Finch	Resident (endemic)
Arremon aurantiirostris	Orange-billed Sparrow	Resident
Arremon crassirostris	Sooty-faced Finch	Resident (endemic)
Arremon brunneinucha	Chestnut-capped Brushfinch	Resident
Arremon costaricensis	Costa Rican Brushfinch	Resident (endemic)
Arremonops rufivirgatus	Olive Sparrow	Resident
Arremonops conirostris	Black-striped Sparrow	Resident
Atlapetes albinucha	White-naped Brush-Finch	Resident
Melozone leucotis	White-eared Ground-Sparrow	Resident
Melozone cabanisi	Cabanis's Ground-Sparrow	Resident (endemic)

Zeledonidae (1)		
Zeledonia coronata	Zeledonia	Resident (endemic)
Icteridae (24)		
Amblycercus holosericeus	Yellow-billed Cacique	Resident
Parulidae (53)		
Seiurus aurocapilla	Ovenbird	Migratory
Oporornis agilis	Connecticut Warbler	Migratory
Geothlypis poliocephala	Gray-crowned Yellowthroat	Resident
Geothlypis tolmiei	MacGillivray's Warbler	Migratory
Geothlypis philadelphia	Mourning Warbler	Migratory
Geothlypis formosa	Kentucky Warbler	Migratory
Geothlypis semiflava	Olive-crowned Yellowthroat	Resident
Geothlypis trichas	Common Yellowthroat	Migratory
Basileuterus rufifrons	Rufous-capped Warbler	Resident
Mitrospingidae (1)		
Mitrospingus cassinii	Dusky-faced Tanager	Resident
Cardinalidae (20)		
Habia rubica	Red-crowned Ant-Tanager	Resident
Habia fuscicauda	Red-throated Ant-Tanager	Resident
Habia atrimaxillaris	Black-cheeked Ant-Tanager	Resident (endemic)
Amaurospiza concolor	Blue Seedeater	Resident
Cyanocompsa cyanoides	Blue-black Grosbeak	Resident
Passerina caerulea	Blue Grosbeak	Resident, Migratory
Passerina cyanea	Indigo Bunting	Migratory
Passerina ciris	Painted Bunting	Migratory
Thraupidae (50)		
Heterospingus rubrifrons	Sulphur-rumped Tanager	Resident (endemic)
Eucometis penicillata	Gray-headed Tanager	Resident
Tachyphonus delattrii	Tawny-crested Tanager	Resident
Ramphocelus sanguinolentus	Crimson-collared Tanager	Resident
Sporophila funerea	Thick-billed Seed-Finch	Resident
Sporophila nuttingi	Nicaraguan Seed-Finch	Resident (endemic)
Emberizoides herbicola	Wedge-tailed Grass-Finch	Resident
Saltator striatipectus	Streaked Saltator	Resident

Resident: reproductive populations in the country; Migratory: no reproductive populations in the country; endemic: species with a world distribution ≤50 000 km^2.
*Numbers next to the family name represent the total species recorded for that family in Costa Rica according to Sandoval & Sánchez (2017)

In general, bird species that currently inhabit early successional vegetation originally had very fragmented distributions since this vegetation was rare in extensive pristine forests; they were restricted to small, ephemeral areas and most of them were randomly distributed within pristine forests. To cope with the characteristics of these habitats, species require a high dispersion capability in order to colonize suitable habitats, when populations increase and reach a maximum density, or when habitats change as ecological succession progresses. Furthermore, bird species associated with early successional vegetation probably had low reproductive success (e.g., low number of eggs or low number of reproductive attempts per breeding season) due to the limited and unstable habitat and food resources.
Cabanis's Ground-sparrow (*Melozone cabanisi*), a Costa Rican endemic species (Chesser et al., 2017; Sandoval, Epperly, Klicka, & Mennill, 2017), exemplifies how changes in land cover can either benefit or affect the distribution of a species. This ground-sparrow originally inhabited natural thickets although it currently inhabits a mix of shade coffee, sugar cane, and squash plantations with tracts of young second growth vegetation (Stiles & Skutch, 1989; Sánchez, Criado, Sánchez, & Sandoval 2009; Sandoval, Bitton, Ducet, & Mennill, 2014). The transformation of forest into agricultural lands during 1800's increased the area of available habitat, the species distribution, and the populations' connectivity; but, the rapid expansion of urbanization after the second half of 1900's transformed the agricultural fields and patches of natural environments into a concrete jungle (Stiles, 1990; Joyce, 2006; Biamonte et al., 2011). As a consequence, the previous, relatively continuous populations of Cabanis's Ground-sparrow are going back to several, small isolated populations; some of them surrounded by an urban matrix that reduces the connectivity between populations and limits the dispersal movements of this ground sparrow (Muñoz, Sandoval, & García-Rodríguez, unpubl. data). How this species will disperse within this new matrix is still unknown, especially considering that many of the natural forested corridors along most rivers and streams have also been eliminated or fragmented during urban development (Joyce, 2006; Biamonte et al., 2011). Therefore, it is expected that urbanized areas function as a barrier or filter that limits gene flow between surviving populations, decreasing the species' fitness and increasing the probability of becoming locally extinct.

Case study 5-Mammals: This case study focusses primarily on the effect of changes in land-use on the distribution of the Southern Cotton Rat, a middle elevation species. Areas covered by early successional vegetation are often too small and isolated to allow large mammals to maintain viable populations within these environments. However, a few small or medium-sized mammal species depend exclusively on these habitats for resources and reproduction. Of the 103 terrestrial mammal species of Costa Rica (Rodríguez-Herrera, Ramírez-Fernández, Villalobos-Chaves, & Sánchez, 2014) early successional vegetation harbors at least eight mice species and two rabbit species; all of them native, including four endemics (Table 3).

TABLE 3
Mammal species that inhabit early successional vegetation in Costa Rica, with information of the species status in the country

Taxa	English name	Endemism
RODENTIA		
Cricetidae - Neotominae		
Scotinomys teguina	Short-tailed Singing Mouse	Resident
Scotinomys xerampelinus	Long-tailed Singing Mouse	Resident (endemic)
*Reithrodontomys rodriguezi**	Rodriguez's Harvest Mouse	Resident (endemic)

*Reithrodontomys sumichrasti**	Sumichrast's Harvest Mouse	Resident
Cricetidae - Sigmodontinae		
Sigmodon hirsutus	Southern Cotton Rat	Resident
Zygodontomys brevicauda	Short-tailed Cane Mouse	Resident
Oligoryzomys costaricensis (=fulvescens)	Costa Rican Colilargo	Resident (endemic)
Oligoryzomys vegetus	Sprightly Colilargo	Resident (endemic)
LAGOMORPHA		
Leporidae		
Sylvilagus gabbii	Central American Tapeti	Resident
Sylvilagus floridanus	Eastern Cottontail	Resident

Resident: reproductive populations in the country; endemic: species with a world distribution ≤ 50 000 km^2.
*The other *Reithrodontomys* spp. in the country are expected to be thicket specialists as well but there is not enough information on the natural history of these species.

These species naturally dwell in dense grasslands or thickets within gaps or along forest edges (often near or along streams) (Monge, 2008; Schai-Braun & Hackländer, 2016; Pardiñas et al., 2017). The dense ground cover of these successional areas offers additional protection from predation to these small, cryptic, and mostly nocturnal species. These species are well adapted to open habitats and if their habitat is disturbed, they can disperse to nearby secondary forests or agricultural fields. Because of the fragmented condition and reduced size of natural thickets, mammal species adapted to these habitats have presumably evolved a high dispersion capacity in response to habitat reduction or resource depletion (Schai-Braun & Hackländer, 2016; Pardiñas et al., 2017).
The Southern Cotton Rat (*Sigmodon hirsutus*), the most common and best-known specialist species in this habitat, might either benefit or be affected by changes in land use. The Cotton Rat originally inhabited tall, dense, grassy or weedy habitats such as savannas and natural pastures (Voss, 2015; Delgado, Aguilera, Timm, & Samudio, 2016), but has gradually expanded its distribution, occupying a mix of agricultural fields, especially sugarcane plantations. Until recently the area of agricultural fields had increased, favoring the expansion of Cotton Rats and other thicket-dwelling species. However, more recently the expansion of urbanization and intensification of pest control practices have reduced populations of thicket-specialist species. In farmlands with intense overgrazing and pest management Cotton Rat populations were also reduced or eliminated (Baker, 1971; Mellink & Valenzuela, 1995; Villafaña-Martín, Silva, Ruiz, Sánchez, & Campos, 1999).
Of the factors affecting the distribution and population size of the Southern Cotton Rat, the expansion of urban areas has likely had the most negative impact, through two non-exclusive processes. First, the expansion of urbanization has drastically reduced the areas occupied by agricultural fields and natural habitats. Second, it has increased interactions with aggressive invasive species associated with urban habitats such as domestic cats and synanthropic introduced rodents (*Rattus* spp. and *Mus musculus*). It is not clear how the interaction of these factors will affect thicket-inhabiting rodents, especially in urban landscapes, but populations are apparently declining and local extinction could be the end point for many populations.

Final remarks

In Costa Rica, urbanization has rapidly accelerated during the last century eliminating large areas of natural ecosystems and forming new artificial habitats (Joyce, 2006; Deák, Hüse, & Tóthmérész, 2016). The early successional vegetation growing in these artificial habitats is the main habitat for a relatively large number of species in several taxa (e.g., plants, butterflies, bees, birds, and mammals). Many of these species are common or exclusive dwellers in these altered environments, which serve as an important reservoir for a group of species that are disappearing due to the rapid elimination of areas covered by successional vegetation.

There has been very little interest in conserving areas covered with successional vegetation, and nearly all efforts have been directed toward protecting pristine environments. This is understandable due to the exuberance and rich diversity found in most pristine environments. However, as shown in the case studies, small tracts of successional vegetation are in most cases the only remnants of nature and they are often immersed in a massive concrete jungle (Cardoso Da Silva & Bates, 2002; Joyce, 2006). Though in most cases these small green tracts include a mix of native and introduced species, they are still important for maintaining populations of many native species and providing resources (e.g., food and shelter) for temporary dwellers.

The rapid expansion of urbanization is eliminating early successional vegetation (Forman, 2014; Johnson & Swan, 2014). As a consequence, many of the plants, insects, birds, and mammals that depend on this type of vegetation are expected to disappear from large parts of their distribution during the next few years (Rodewald & Gehrt, 2014; Ramírez-Restrepo & MacGregor-Fors, 2017). Our knowledge of urban successional habitats is scarce, fragmentary, and for the most part anecdotal. This limits our understanding of important biological processes such as dispersal movement, reproductive success, and effects of isolation, particularly for specialist species. However, the extensive knowledge of forest fragments provides some insights to the approach that should be taken to avoid or at least reduce the depletion of species from the already threatened urban successional habitats (Barrantes, Ocampo, Ramírez-Fernández, & Fuchs, 2016). A priority in this direction will be to protect natural and semi-natural early successional vegetation, and enhance their connectivity. Green corridors between woodlots (sources of species) and domestic gardens have largely enhanced species richness of staphylinid beetles in gardens (Vergnes, Le Viol, & Clergeau, 2012; Klaus, 2013). The diversity of freshwater insects (e.g. dragonflies) increased by improving the quality of river banks (Weber, García, & Wolter, 2017). With a little effort small, species-depauperate areas can be rapidly colonized by opportunistic species (see Case study 1). These small areas maintain populations of plants and arthropods, and could function as stepping stones for colonization by specialist species (Uezu, Beyer, & Metzger, 2008).

Finally, we encourage biologists to generate more information on the biology of organisms specialized for living in early successional vegetation in urban areas. Knowledge of the distribution and connectivity, as well as the phenological patterns, population size, response to habitat reduction, and general ecology of organisms restricted to this habitat are necessary for proposing effective conservation actions. Additionally, information about species that inhabit early successional vegetation may contribute to people from urban areas to regaining contact with the natural world and to appreciating the surrounding biodiversity. Certain groups of plants and animals that inhabit early successional vegetation may provide an opportunity for urban residents to learn more about biology and appreciate the beauty of the natural world, which in turn facilitates conservation.

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