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Effects of Secondary Forest Succession on Amphibians and Reptiles: A Review and Meta-analysis

Michelle E. Thompson¹ and Maureen A. Donnelly¹

Over the past century, humans have cleared the Earth's forests at an alarming rate and intensity. The majority of global forest cover is categorized as secondary forest, and it is becoming increasingly important to consider secondary forests in addition to old-growth forest in conservation planning for biota. We reviewed the literature to synthesize information on amphibian and reptile communities during secondary forest succession. We summarized literature on mechanisms of community change during forest succession and conducted a meta-analysis to estimate effect sizes for species richness and abundance in human-modified landscapes (agriculture, pasture, and plantation) and old-growth forests compared to regenerating secondary forests. Studies reported strong support for differences in species composition among human-modified landscapes, secondary forest, and old-growth forest as well as species-specific responses to successional forest change. Secondary forest generally had higher species richness and abundance than human-modified landscapes, but lower species richness and abundance than old-growth forests. This result was more pronounced in amphibians than reptiles, and effect size of abundance was more variable than richness among studies. Secondary forests have better conservation value than altered habitats, but they do not necessarily hold the same conservation value for species as old-growth forest.

THE extensive degradation of natural systems caused by anthropogenic activities is a pressing global conservation concern (Raven and Wilson, 1992; Williams and Nowak, 1993; Sodhi et al., 2008). There is hope that some of the negative impacts caused by forest loss such as reduction of ecosystem services and loss of biodiversity may be offset by the regeneration of altered landscapes to secondary forests (Pearce, 2001). However, the value of secondary forests to fauna is poorly understood (Gardner et al., 2007a). Over 60% of the world's forests are degraded or are recovering from a major disturbance (FAO, 2015; Fig. 1), and in some regions of the world, secondary forest cover is increasing (Aide and Grau, 2004). Thus, understanding the role, structure, and function of secondary forests in supporting biodiversity is critical for wildlife in the future.

For decades, there has been a consistent trend of loss in global forest cover. However, in many regions of the world, forest loss is partially mitigated by secondary forest regeneration (Keenan et al., 2015). Shifting social, political, and economic trends are driving reduction in forest cover loss and secondary forest gain. As a consequence of reduced deforestation and an increase in forest regeneration, the global rate of forest loss was reduced by over 50% between the periods of 1990–2000 and 2010–2015 (FAO, 2015). Many countries are experiencing trends of rural to urban migration (Grau et al., 2003; Barbieri and Carr, 2005; McDonald, 2008), changes in forest and conservation policy (Southworth and Tucker, 2001; Kull et al., 2007), or are developing ecotourism (Kull et al., 2007), resulting in abandonment of agriculture and pasture land and promoting natural regeneration and formation of protected areas (Aide and Grau, 2004; Aide et al., 2012).

One of the main consequences of deforestation is biodiversity loss (Brook et al., 2003; Gibson et al., 2011). Worldwide declines have been reported for amphibians and reptiles (Houlahan et al., 2000; Wake and Vredenburg, 2008), and habitat destruction is one of the primary contributing factors to declines (Stuart et al., 2004; Reading et al., 2010; Böhm et al., 2013). Approximately one third of amphibian species are listed as threatened on the IUCN red list (IUCN et al., 2008). Although a full assessment for reptiles has not yet been completed, it is estimated that somewhere between 15% and 36% of reptiles qualify as threatened by IUCN standards (Böhm et al., 2013). The ecological requirements and physiological limitations of amphibians and reptiles make these animals sensitive to environmental changes such as altered vegetation structure and microclimates after deforestation.

In many animal taxa, species richness recovers asymptotically as forest matures, and recovery has been found to occur in approximately the same amount of time as recovery of tree species richness (Dunn, 2004). Thus, the ecological values of secondary forest to fauna may largely depend on the trajectory of vegetation regrowth. For plant species, overcoming the challenges of recolonization involves species overcoming biotic (e.g., competition with exotic species) and abiotic legacies (e.g., altered soil nutrient content, altered hydrology) of disturbance that can vary considerably as a result of disturbance type (e.g., large-scale hurricane, agriculture, pasture), disturbance intensity, and surrounding landscape matrix (e.g., proximity to patches of remnant forest; Lucas et al., 2002; Cramer et al., 2008). The factors that may contribute to recovery of amphibians and reptiles during secondary succession include dispersal to secondary forest, changes in forest structure, temperature and humidity, competition, and prey, predator, and parasite fluctuations

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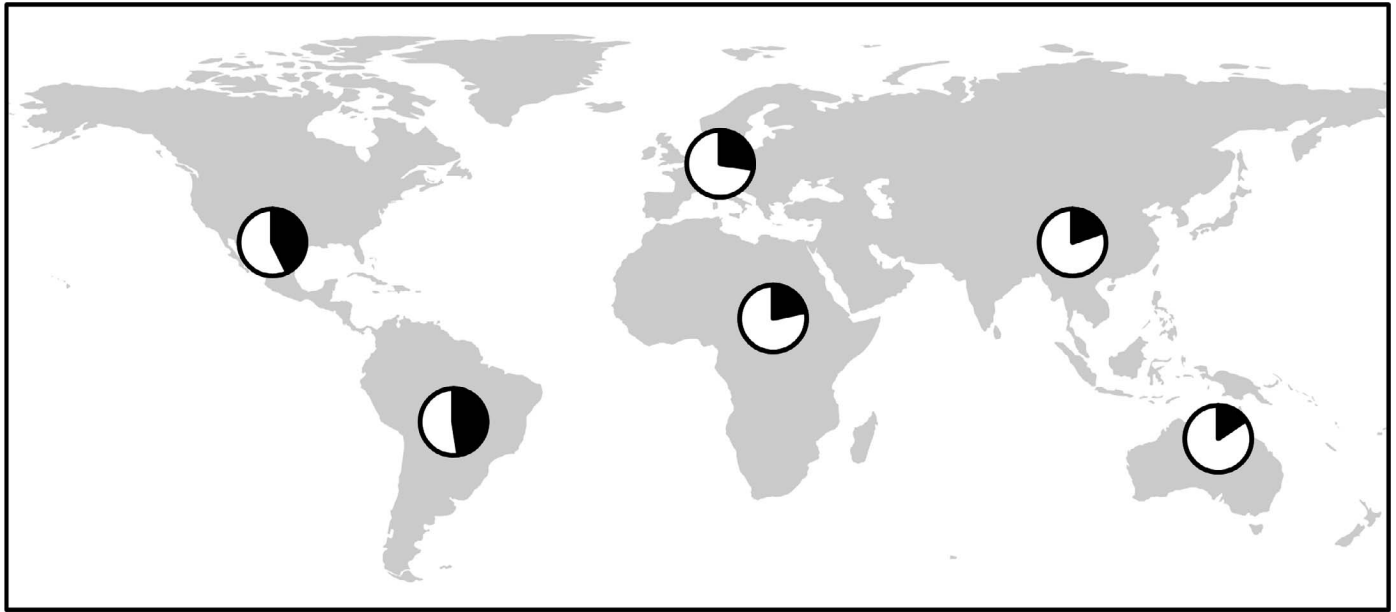


Fig. 1. Map of percent of primary forest (black) and other naturally regenerated or planted forests (white) as defined by FAO (2015) by continent.

over the course of forest succession, all of which are directly or indirectly affected by the course of regeneration of the vegetation.

Across animal taxa, there is support for lower diversity in secondary forests than in old-growth forests (Gibson et al., 2011). Often, species composition differs between secondary and old-growth forests. Subsets of old-growth specialist species are absent from secondary forests (Luja et al., 2008; Chazdon et al., 2009; Gibson et al., 2011; Hernández-Ordóñez et al., 2015) but begin to recover as the forest ages (Chazdon et al., 2009). In some cases, recovery can result in new forests with new combinations of species in comparison to historical sites (Lugo and Helmer, 2004). While secondary forests have been found to be a valuable habitat for a wide array of species, species' use of secondary forests is extremely variable among species and sites differing in land use history (Janzen, 2002; Bowen et al., 2007).

These highly variable species responses to forest succession are reflected in the literature on recovery of amphibian and reptile communities. For example, some authors have found similar species richness (Herrera-Montes and Brokaw, 2010; Hilje and Aide, 2012; Cortés-Gómez et al., 2013), while others have found higher species richness in old-growth forest compared to secondary forests (Petranka et al., 1993, 1994; Vallan, 2002; Pawar et al., 2004; Scott et al., 2006; Gardner et al., 2007a; Basham et al., 2016). For abundance, studies have reported similar (Corn and Bury, 1991; Gardner et al., 2007a), lower (Lieberman, 1986; Heinen, 1992), and higher total community abundance in old-growth forest compared to secondary forest (Petranka et al., 1993; Crawford and Semlitch, 2008; Luja et al., 2008). Measures of total abundance and species diversity tend to be variable, but there is an emerging consensus on changes in species composition and interspecific differences in abundance (Ernst and Rödel, 2006; Gardner et al., 2007a; Ficetola et al., 2008; Hawkes and Gregory, 2012; Beirne et al., 2013; Guerra and Aráoz, 2015; Hernández-Ordóñez et al., 2015). There is a distinct difference in amphibian and reptile composition between secondary forest and anthropogenic land use (Gardner et al., 2007a; Luja et al., 2008; Gillespie et

al., 2012; Bruton et al., 2013; Cortés-Gómez et al., 2013; Guerra and Aráoz, 2015) and between secondary forest and old-growth forest (Luja et al., 2008; Cortés-Gómez et al., 2013; Hernández-Ordóñez et al., 2015).

The dominance of secondary forest cover is ubiquitous across continents (Fig. 1). However, we currently have poor knowledge of patterns of and mechanisms of community assembly in secondary forests. To better understand general trends of amphibian and reptile communities in secondary forests, we conducted a review and meta-analysis of the literature. We summarized published literature on mechanisms that drive amphibian and reptile community change during secondary forest succession and conducted a meta-analysis of published studies on amphibian and reptile community recovery in secondary forests to determine the overall effect sizes of amphibian and reptile richness and total abundance in old-growth forest and human-modified landscapes (agriculture, pasture, and plantation) compared to secondary forests. We hypothesized that amphibian and reptile species richness and abundance would be higher in secondary forest than human-modified landscapes and lower in secondary forests than in old-growth forests.

MATERIALS AND METHODS

Literature search.—We searched the database Thompson ISI Web of Knowledge (all years through March 2017) for keywords “herpetofauna” or “amphibian*” or “reptile*”, in combination with “secondary forest” or “secondary succession” or “forest regeneration” or “regenerating forest” or “logging”. In addition, we searched the literature cited sections of relevant papers found through the database search.

Literature summary of mechanisms.—As a consequence of the lack of research that explicitly tests mechanistic drivers to amphibian and reptile community change during forest regeneration, we were unable to conduct a formal meta-analysis. Instead, we summarized abiotic and biotic trends in secondary forest succession that have the potential to act as mechanisms for amphibian and reptile community change

during secondary forest succession and discussed results of the few studies that have tested support for these mechanisms.

Meta-analysis.—The term ‘secondary forest’ encompasses many land use types ranging from forests regenerating from complete clearing of land for another use to moderate human use for selective logging and agriculture. For our meta-analysis, we defined secondary forest as forest that had been completely cut and was undergoing natural regeneration. We compiled data on estimated time to recovery for species richness for studies that conducted research in different age classes of secondary forest (at least two different replicated age classes of secondary forest) and reference sites (old-growth forest). We calculated “recovery time” as the age or age class reported by the literature where species richness in secondary forest was not significantly different from reference sites.

To calculate effect size of community parameters across studies (average species richness and average abundance of total community), we included studies that compared secondary forest with undisturbed reference sites or a human-modified land use (agriculture, pasture, and plantation) and that used standardized sampling techniques, replication, and reported values on species richness and abundance. We combined all human-modified habitats together in one category because we found too few studies to analyze each type of modified habitat separately. We used reported values of average species richness and average total abundance and standard deviation or we calculated values using data extracted from tables and figures. We calculated the effect sizes across studies by using the log-transformed ratio of means (Hedges et al., 1999). Because we were interested in how anthropogenic land use and reference sites compared to secondary forests, we calculated effect size as the natural log of the ratio of average species richness or average total community abundance in a given land use or undisturbed natural habitat to species richness or abundance in secondary forest. Negative values indicate average species richness or abundance was lower in old-growth forest or human-modified habitat than in secondary forest. We conducted analysis using the ‘escal’ function and random-effects models with the restricted maximum likelihood estimator in package ‘metafor’ (Viechtbauer, 2010) in R v3.3.1 (R Core Team, 2016).

RESULTS

Literature summary of mechanisms

Dispersal.—Before any other mechanisms driving community assembly in secondary forests can take place, species must first disperse to secondary forest sites. Compared to other taxa such as birds and mammals, amphibians and reptiles are generally more limited in dispersal capability (Hillman et al., 2014), and limited dispersal may limit their ability to colonize secondary forests. Dispersal is largely affected by geographic distance between patches (Brown and Kodric-Brown, 1977; Ficetola and De Bernardi, 2004), type of matrix between patches (Fahrig and Merriam, 1994; Gascon et al., 1999; Nowakowski et al., 2013), and species-specific behavior and physiology (Lees and Peres, 2009). Species that are highly mobile and resilient to matrix conditions will be more successful in colonizing isolated secondary forest patches. For amphibians and reptiles, differences in microclimates, predation rates, and movement through substrate type can

affect dispersal through matrix habitat (Nowakowski et al., 2015; Kay et al., 2016). However, studies on amphibians and reptiles rarely explicitly incorporated matrix type or distance of secondary forest to old-growth forest in analyses (but see Hilje and Aide, 2012).

Forest structure.—Compared to old-growth stands, secondary forests have been found to differ in vegetation structure and leaf litter structure (Lebrija-Trejos et al., 2008; Letcher and Chazdon, 2009; Chazdon, 2014) which are thought to be important habitat components that regulate amphibian and reptile community composition and density (Lieberman, 1986; Heinen, 1992; Herrera-Montes and Brokaw, 2010; Whitfield et al., 2014). The structure of forest vegetation provides species with microhabitats for perching, foraging, breeding, and fleeing predators. Additionally, forest structure and leaf litter structure mediate temperature and humidity on the forest floor; the leaf litter layer is an important habitat feature for amphibians and reptiles in forests. As secondary forest ages, and forest structure becomes more similar to that of old-growth forest, secondary forest may provide more suitable habitat for amphibian and reptile species that are dependent on the characteristics of old-growth forest. Early stages of secondary forests (<20 years after disturbance) tend to have low plant diversity (Letcher and Chazdon, 2009) and young trees, of similar age and size (Budowski, 1965), providing a uniform habitat of canopy height and perch diameter, and in some studies of herpetofauna in secondary forests, these vegetation characteristics have been linked to change in amphibian and reptile communities. For example, vegetation structure features such as canopy cover and abundance of woody plants (Cortés-Gómez et al., 2013; Hernández-Ordóñez et al., 2015) have been linked to amphibian and reptile community composition. In young secondary forests, there is an absence of large, mature buttressed trees, and there is less coarse woody debris on the forest floor (Kissing and Powers, 2010) than in old-growth forests which are microhabitats that some amphibian and reptile species specialize on (e.g., *Norops humilis* in Central American tropical forest [Fitch, 1973] and *Ensatina eschscholtzii* in the Pacific Northwest of the United States [Jones and Aubry, 1985; Butts and McComb, 2000]). Additionally, absence of trees in riparian zones following clearing can also increase sedimentation in streams that may affect amphibian stream communities (Corn and Bury, 1989). Depth of leaf litter is known to affect densities of amphibians and reptiles (Whitfield et al., 2014), and therefore fluctuations in leaf litter among successional stages can also influence community composition. For example, Ash (1997) found that plethodontid salamander abundance returned in concurrence with return of the leaf litter layer. However, leaf litter fall and depth has been shown to recover rapidly during secondary forest succession (Oliviera, 2008; Ostertag et al., 2008), so leaf litter depth may have a greater effect on species composition and abundance in very early stages of regeneration than in later stages of succession.

Temperature and humidity.—As secondary forest ages, temperature decreases and humidity increases (Lebrija-Trejos et al., 2011). Response of ectothermic animals, such as amphibians and reptiles, to habitat change is thought to be influenced by changes in temperature (Tuff et al., 2016). Regulation of body temperature is important for amphibians and reptiles because temperature affects growth, reproduction (Hillman et al., 2009), ecological interactions, and



Fig. 2. Map of study sites included in meta-analysis by country. Black dots indicate the study locations. Points jittered in the northwestern United States to show overlapping locations.

disease susceptibility in ectotherms (Woodhams et al., 2003; Pounds et al., 2006). Additionally, for amphibians, humidity influences distribution because the highly permeable skin of amphibians increases their vulnerability of desiccation, particularly for species that oviposit terrestrially (Duellman, 1988; Hillman et al., 2009). The eggs, surrounded by a gelatinous coat, are also vulnerable to desiccation. Many studies that conducted amphibian and reptile surveys over the course of forest succession suggest that temperature and humidity likely play a large role in the described patterns of amphibian and reptiles they observed (Lieberman, 1986; Welsh, 1990; Heinen, 1992; Vallan, 2002; Rios-López and Aide, 2007; Herrera-Montes and Brokaw, 2010; Hernández-Ordóñez et al., 2015). One study found that forest structure explained the variability in microclimatic data and microclimate explained best the variation in herpetofaunal diversity (Herrera-Montes and Brokaw, 2010). Rittenhouse et al. (2008) found reduced juvenile anuran survival in recent clear-cut areas because of desiccation, but brush piles helped mitigate negative effects of logging by providing cool, humid microhabitats for amphibians. Despite the general consensus that microclimate likely plays a large role in community assembly, there is a lack of research that specifically tests for temperature and humidity as mechanisms for species response to forest succession.

Biotic factors.—Biotic factors such as the effect of prey and predator fluctuations, competition, and parasitism are known to affect species distributions at both local and broad spatial extents (Wiszniewski et al., 2013). In studies in secondary forests, much less attention has been paid to biotic factors compared to abiotic factors. Competition between ecologically close species has been found to increase with increasing levels of human disturbance (Luiselli, 2006). However, Ernst and Rödel (2006) tested the importance of competition in community organization in secondary forests and did not find evidence for competition shaping species assemblage of anurans in regenerating forests. Arthropods, common prey for amphibians and reptiles, change in abundance and diversity during secondary forest succession, but communi-

ties are similar to those in old-growth forests after about 25–50 years (Floren and Linsenmair, 2001; Osorio-Pérez et al., 2007; Hopp et al., 2010). Changes in prey abundance may not only affect composition and abundance of species but can also affect behavior. For example, Greene et al. (2008) found that terrestrial prey abundance for salamanders was lower in late successional forests than early successional forests, causing salamanders to move farther from streams to forage in late successional sites. Predator assemblages change over the course of secondary forests regeneration (e.g., birds: Borges, 2007; Karthik et al., 2009). Therefore, it is likely that predation rates differ during forest regeneration. However, little is known about amphibian and reptile predation rates during forest succession.

Meta-analysis

A total of 24 studies met our requirements for meta-analysis of species richness and total abundance in land use, secondary forests, and old-growth forests (Supplemental Appendix A; see Data Accessibility). Sixteen studies included amphibians and 14 included reptiles. Studies were conducted across the globe but mostly clustered in North America, South America, and Australia (Fig. 2). There was an even distribution of age classes of secondary forests included in studies, but 17% of studies did not include information on age of secondary forest (Fig. 3). Estimates for time to recovery for species richness in secondary forest varied from 10–16 years to more than 80 years of regeneration (Fig. 4).

The effect size across all studies for average amphibian species richness was significantly higher in undisturbed habitats compared to secondary forests. Sites with other types of land use had significantly lower species richness than secondary forests (Fig. 5). However, there was no significant difference in abundance of amphibians between secondary forest and sites of anthropogenic land use. For reptiles, we did not find statistically significant trends in species richness. Results show only a suggestive trend of a positive effect of old-growth forest and negative effect of modified habitat on species richness compared to secondary

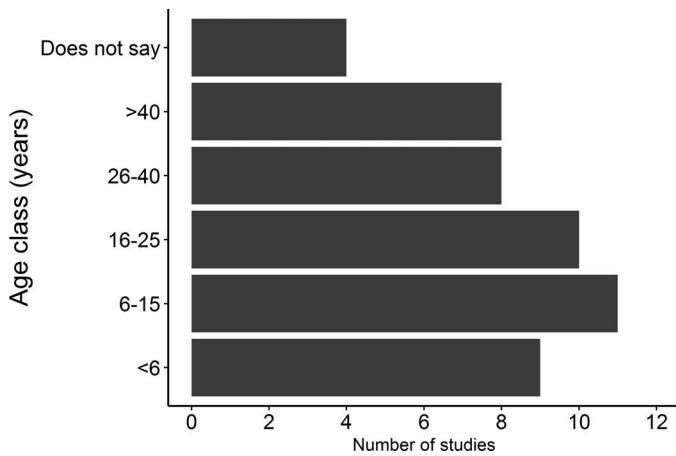


Fig. 3. The age distribution of forest included in 20 of the published articles included in the meta-analysis. Four studies did not provide information on secondary forest age.

forest (Fig. 5). We did not find any trends in the comparison of average abundance among secondary forest and old-growth forest and human-modified land use sites for reptiles; there was substantial variation among studies (Fig. 5).

DISCUSSION

With increasing reliance on secondary forest for conservation planning and maintaining biodiversity, it is imperative that we understand how animal communities assemble over the course of forest regeneration. Here, we report the state of knowledge on amphibian and reptile community response over the course of secondary forest succession and summarize information on potential mechanisms for observed patterns in the literature. We found that, in general, old-growth forest tends to have more species than secondary forest and human-modified habitat less species than secondary forest. Secondary forests have better conservation value than altered habitat, but they do not necessarily hold the same conservation value for species as old-growth forest.

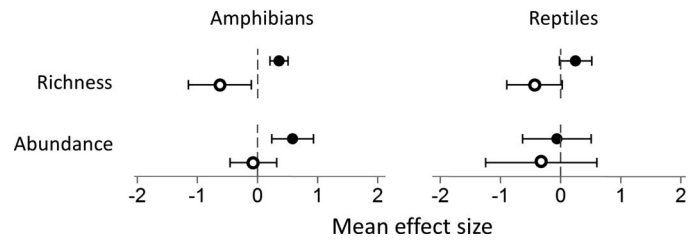


Fig. 5. Mean effect sizes (and 95% CIs) for the comparison of amphibian and reptile mean species richness and mean abundance in secondary forest to old-growth forest (closed circles) and human-modified habitat (open circles). Response ratios were calculated as the natural log of the ratio of average species richness or average abundance in a given human-modified land use or old-growth forest habitat to species richness or abundance in secondary forest. Negative values indicate average species richness or abundance was lower in areas of old-growth forest or human-modified habitat than in secondary forest. For amphibian richness: $N_{old-growth} = 10$, $N_{land use} = 5$, and for reptile richness: $N_{old-growth} = 11$, $N_{land use} = 7$. For amphibian abundance: $N_{old-growth} = 10$, $N_{land use} = 6$, and for reptile abundance: $N_{old-growth} = 9$, $N_{land use} = 7$.

However, there was substantial variation among studies, especially for reptiles. Our finding of significant differences in community response to secondary forest succession for amphibians but not reptiles suggests that amphibians and reptiles may be affected differently by environmental factors associated with secondary forest succession and supports why they should be considered separately in studies of communities, ecosystems, and landscapes.

Secondary forests provide suitable habitat for many amphibian and reptile species, but there is substantial variation in time to recovery of the animal community. Several studies reported that amphibian and reptile communities recover relatively rapidly. Others reported a period of at least 80 years to recovery (Fig. 4). However, in these forests that are deemed “recovered,” secondary forests may have similar species richness as old-growth forests but secondary forests may not provide suitable habitat for every species in the regional species pool. Some species appear to be unique

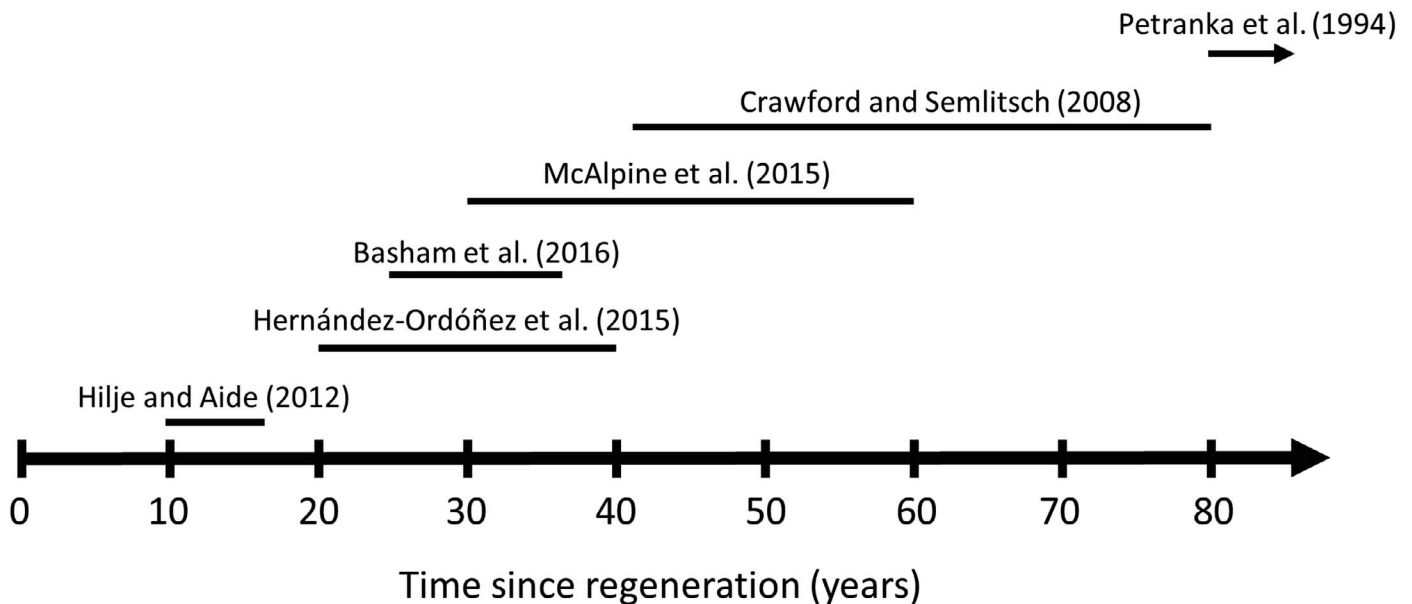


Fig. 4. Published estimates of time to recovery (years) of amphibian and reptile species richness. Arrow under Petranka et al. (1994) indicates that more than 80 years were required for species richness to recover.

only to old-growth forests (Barlow et al., 2007; Luja et al., 2008; Gibson et al., 2011). It is critical to identify the old-growth specialists in order to make appropriate conservation decisions for species most at risk. Additionally, it is unclear if amphibian and reptile populations in secondary forest patches are being maintained by internal recruitment, immigration from nearby mature forest, or a combination of the two processes. Although secondary forests do not provide suitable habitat to maintain populations of some species, they may still have other positive effects in comparison to matrix habitat such as increasing connectivity between older forest patches, providing less resistance to movement than matrix habitat, and acting as good corridors for dispersal (Nowakowski et al., 2013).

In some cases, land-use legacy and current surrounding landscape conditions may cause the trajectory of community assembly to vary from historic old-growth conditions. The variation in recovery trajectory has been recorded in plant communities (Janzen, 2002; Cramer et al., 2008). Time to recovery for a forest can also depend on the life zone. In the tropics, vegetation in dry forest recovers more rapidly than wet forest, and cloud forest recovers the slowest of the three forest types (Janzen, 2002). The variation in vegetation trajectory and recovery time is likely to affect amphibian and reptile communities. For example, a species may be less inclined to disperse through or populate a pasture or early stage secondary forest in lowland wet forest habitat than in lowland dry forest habitat because the microclimate conditions in the recently modified landscapes and old-growth forests sites are substantially more disparate in lowland wet forests than dry forests (i.e., hot, dry microclimates; Janzen, 2002).

Not all species in a community respond the same over the course of secondary forest succession. There was a common trend across studies of species-specific effects. These species-specific effects are likely a contributing factor in why many studies found statistically nonsignificant effects between treatments and reference sites and why we found such variation in effect size across studies, especially for the measure of total abundance. Species that are disturbance specialists can weaken observed effects for whole community analysis (Thompson et al., 2016). Some trends in interspecific differences can be explained by particular ecological traits such as tolerance to harsh microclimates, breeding requirements, and other habitat associations. Species that are more resistant to desiccation (Ash, 1997) and species with high thermal tolerances and metabolic rates (Rios-López and Aide, 2007) can tolerate recently disturbed habitats that have high solar irradiation and warm, dry microclimatic conditions. Arboreal species of amphibians (Rios-López and Aide, 2007) and reptiles (Enge and Marion, 1986) increase in abundance and diversity with the return of woody vegetation. One of the most evident trends in the relationship between species traits and forest succession is effect of breeding habitat of anurans. Species with specific breeding habitats and with terrestrial breeding habits are more confined to old-growth forests (Vallan, 2002; Gardner et al., 2007b) whereas pool-breeding species are often able to exploit matrix habitat (Tocher et al., 2002). Terrestrial breeding anurans will likely be one of the groups most at risk in coming decades because of their adverse response to both habitat change (Nowakowski et al., 2017) and climate change (Donnelly and Crump, 1998). However, the presence of many terrestrial breeding anurans in later stages of secondary forest provides

hope that secondary forest sites can eventually provide suitable habitat to maintain diversity of these species.

One of the main findings of our review is that there are enormous gaps in the understanding of amphibian and reptile community assembly over the course of secondary forest succession. In addition to calling attention to the dire need for more research, we suggest several recommendations for future studies. First, researchers should pay careful attention to study design. We found few studies that focused on amphibians and reptiles in secondary forest that had well-constructed experimental design, controls, and replication to adequately test hypotheses (and see review by Gardner et al., 2007b). Second, in future studies it is important to try to understand underlying causes of variation and explicitly test mechanisms driving trends in community change. Past studies characterize community patterns over the course of forest regeneration and suggest hypotheses to explain observed patterns. Future work should focus on the underlying processes generating the patterns and to evaluate the strength of mechanisms relative to one another. Success in planning conservation strategies not only depends on knowledge of patterns but the mechanisms driving the patterns (Cushman, 2006; Gardner et al., 2007a). Lastly, it is important to establish long-term research projects. Although several long-term studies on vegetation regeneration in secondary forest exist (Burslem et al., 2000; Sheil, 2001; Chazdon et al., 2007), we know of no long-term research on amphibians and reptiles along the course of secondary forest succession. Many studies stretch over one or two field seasons (one or two years) and substitute space for time by using chronosequences. While these methods are valid and provide valuable inference, ideally, long-term research programs should be established to tease out ecological trends from stochastic fluctuations, detect gradual changes, and detect small but biologically relevant effect sizes.

Future conservation management planning will have to use approaches that integrate the conservation of remaining patches of old-growth forest and surrounding secondary forests to preserve the greatest biodiversity possible. To integrate predictions of the value of secondary forest for a given conservation area, we first need to know for what species secondary forest can provide habitat that can maintain stable populations, and what the most important habitat features are to species at risk of decline. Secondary forest is the dominant global forest cover, is increasing in some regions, and it has been posed that secondary forest may mitigate for biodiversity loss from deforestation (Wright and Muller-Landau, 2006). However, the potential of secondary forests to serve as safety nets for biodiversity is the subject of formidable debate (Laurence, 2007). We still do not know to what extent secondary forest may mitigate for species loss, especially for relatively understudied taxa like amphibians and reptiles. It is urgent to evaluate the capability of secondary forests to host biodiversity comparable to old-growth forests and understand the mechanisms by which communities assemble in secondary forests, especially for taxa at high risk of extinction such as amphibians and reptiles.

DATA ACCESSIBILITY

Supplemental material is available at <http://www.copeiajournal.org/ch-17-654>.

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