

Recolonization of secondary forests by locally extinct fauna through the lens of range expansion: Four open questions

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Even though deforestation is ongoing particularly in the tropics (Roberts et al., 2021), recovering tropical forests are becoming a prevalent component of the Anthropocene landscape. This recovery is in part due to socioeconomic changes leading to the abandonment of agricultural fields (Aide et al., 2013; Aide & Grau, 2004). These abandoned fields undergo ecological succession developing complex forest structures that, given the appropriate conditions, eventually provide the minimum requirements for the recolonization of locally extinct fauna. The resulting biodiversity patterns following this recolonization process have been well described in the empirical literature and synthesized in at least nine reviews or meta-analyses (Acevedo-Charry & Aide, 2019; Bowen et al., 2007; Chazdon, 2014; Dent & Wright, 2009; Dunn, 2004; Hughes et al., 2020; Lennox et al., 2018; Lindenmayer & Hobbs, 2004; Thompson & Donnelly, 2018). The general patterns are clear. Animal species richness can recover quickly after abandonment depending on geographical region, landscape attributes, and degree of disturbance (Dunn, 2004). However, animal species composition takes longer, with some forest specialists and functional groups missing from secondary forests (Acevedo-Charry & Aide, 2019). After the synthesis of these general fauna recolonization patterns still much remain unknown about the eco-evolutionary mechanisms that drive these patterns.

Range expansion theory is commonly invoked to describe the eco-evolutionary mechanisms that drive multiple types of population expansions. This theoretical framework has the potential to contribute to our understanding of fauna recolonization of

secondary forests. Here we describe four open questions about population-level processes driving secondary forest recolonization of locally extinct fauna through the lens of range expansion. We synthesize these ideas with the aim of providing a framework to guide future research.

1 | FOUR OPEN QUESTIONS

1.1 | Do dispersive traits characterize early recolonizing individuals?

A null hypothesis would state that early recolonizing populations would be composed of a random subset of individuals from old-growth forests that disperse via a simple diffusive process (Figure 1a; Okubo & Levin, 2001). Alternatively, range expansion theory predicts an overrepresentation of long-distance dispersers at the expansion front. This pattern is also known as a pulled expansion because the dynamics mostly imposed by individuals at the expansion front are the ones "pulling" the population spread (Figure 1b; Gandhi et al., 2016). Morphologically, these dispersive individuals at the edge may exhibit longer limbs, larger body sizes, or better body condition (Chuang & Peterson, 2016). These dispersive traits allow individuals to move quicker through difficult matrices, experiencing less mortality during transit. Behaviorally, traits associated with exploratory or aggressive personalities may also be advantageous (Canestrelli et al., 2016; Cole & Quinn, 2012). These

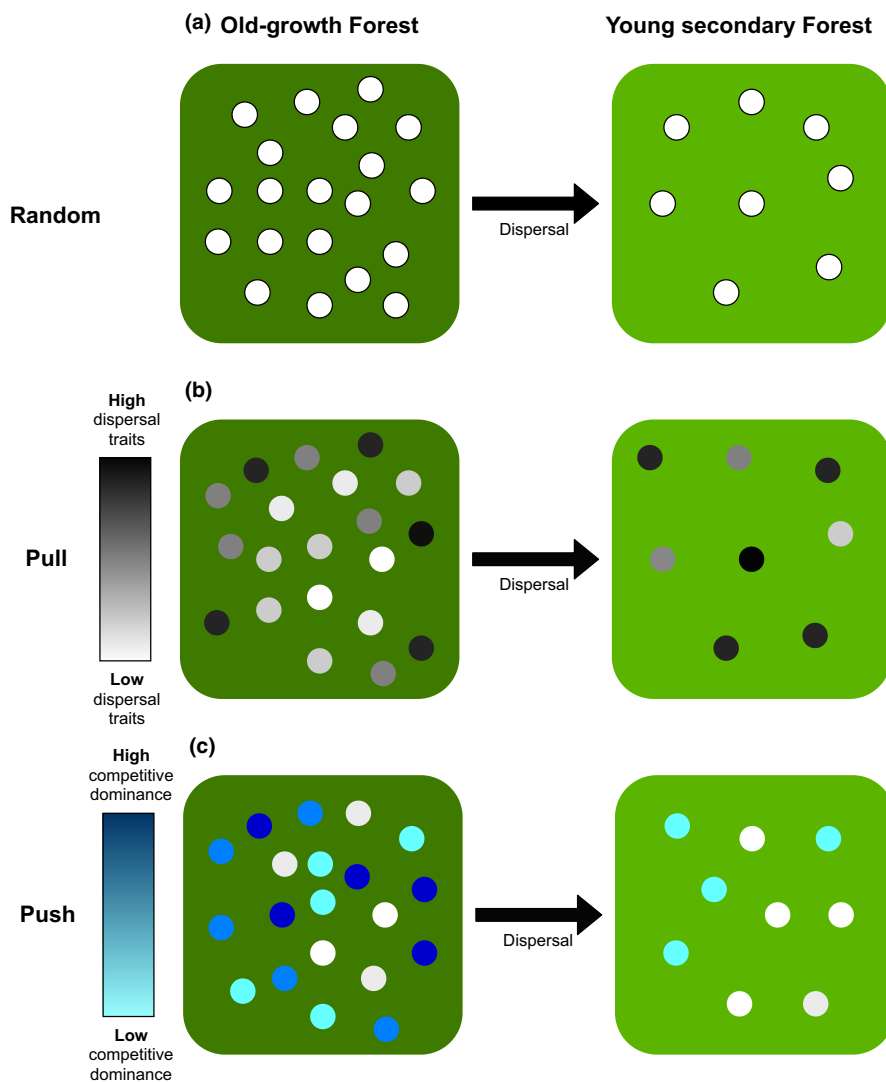


FIGURE 1 Recolonization of secondary forests happens when individuals disperse from a nearby source of old-growth forest populations. This pattern of recolonization could be (a) the result of a random subset of individuals dispersing and colonizing nearby secondary habitats. Instead, the set of recolonizing individuals may not be random but have a particular set of characteristics. (b) Old-growth source populations could show spatial sorting where highly dispersive individuals (those with larger limbs or exploratory and aggressive behavior) are overrepresented in the forest patch edges and more likely to colonize nearby patches. These are often known as “pull” expansions because highly dispersive individuals living at the edge of the source population are the ones “pulling” the expansion. Alternatively, (c) because old-growth populations are expected to be at carrying capacity recolonization may be driven by subordinate individuals that cannot outcompete dominant conspecifics and disperse looking for alternative territories. This is the case of “push” expansions when dispersal is driven by these subordinate individuals that are pushed away due to density dependence.

exploratory or aggressive individuals would be better adapted to identify novel feeding resources, establish new territories, and overcome negative Allee effects that would reduce reproductive output in low-density scenarios (see below). Multiple empirical examples of these patterns exist in invasive toads and insects (e.g., Phillips et al., 2006). Still, early recolonizing individuals in secondary forests may not necessarily exhibit dispersive traits if recolonization is the result of pushed expansions (Figure 1c). Old-growth forests are assumed to be at carrying capacity and individuals may disperse to nearby secondary forests when the cost of dispersal is less than the cost of competition, predation, or parasitism in the source population (Clobert et al., 2009). These expansions are so named because density dependence “pushes” subordinate individuals to the edge of the population.

There are also potential trade-offs between the individual traits that favor dispersal and those that provide adaptability to young secondary forests (e.g., Perkins et al., 2016). During recolonization, animals move from large old-growth forest patches with closed canopies, relatively lower temperatures, and larger trees to nearby smaller young secondary forest patches with open canopies, higher

temperatures, and smaller trees (Rios-López & Mitchell Aide, 2007). Therefore, recolonizing populations must balance the benefits of dispersive traits with those that benefit their likelihood of successfully establishing in areas with sub-optimal environmental conditions.

1.2 | Do recolonizing populations experience density-independent growth?

Animal populations recolonizing secondary forests in small numbers can experience *r*-selected environments due to less density regulation (Burton et al., 2010). Higher population growth rates can occur consequently from decreased density dependence, but also due to shifts in life-history strategies such as larger clutch sizes, early-season breeding, and a higher breeding probability of smaller females (Phillips, 2009). The duration of these density-independence conditions would be contingent on population growth rates, carrying capacity, and the level of connectivity to old-growth forest sources. While recolonizing in small numbers may have the benefit of reduced density regulation, at the initial stages of recolonization these

small populations can also be vulnerable to demographic stochasticity, loss of genetic diversity, and inbreeding (Hundertmark & Van Daele, 2010; see below). These patterns may vary by species. For instance, these patterns may well apply to *r*-selected species that generally have small bodies; however, the consequences of density independence may be less pronounced in large-bodied mammals.

1.3 | Do recolonizing populations experience escape and release from coevolved natural enemies?

Recolonizing populations of secondary forests are expected to experience less parasitism because they recolonize in small numbers (Phillips et al., 2010). Escaping from parasitism would allow individuals to invest more resources in reproduction, which combined with low-density regulation, can result in higher population growth rates (Perkins et al., 2008). The rate of parasitism in an already small parasite population would decrease in subsequent generations due to small host densities and stochastic events reducing effective transmission (Chan et al., 2015). Still, the escape and release from parasites do not last forever. The duration of the parasite escape and release will be contingent on the degree of connectivity to old-growth forest sources. Parasites will continue to arrive and eventually adapt to better exploit hosts living in secondary habitats. Over time, parasite infection would complement density dependence to regulate the population (Stricker et al., 2016). Similar ideas could apply to other types of enemy-victim systems (*sensu* Holt & Barfield, 2009).

The consequences of generalist parasites on recolonizing populations may be fundamentally different. Generalist parasites are commonly associated with small fragments or early successional stages (Froeschke et al., 2013). Typically, these generalist parasites are more virulent, have higher transmission rates, and inhabit larger spatial ranges because they can exploit a variety of host species (Leggett et al., 2013). Moreover, rates of parasitism may increase in secondary forests if nutritional resources for the host are sub-optimal decreasing host body condition (Coop & Kyriazakis, 2001). The effect of poor nutrition could be amplified if recolonizing individuals are subordinate individuals who lack the parasite tolerance or resistance that often characterizes dominant individuals (Medzhitov et al., 2012). Therefore, hypothesized patterns of parasitism in recolonizing populations would depend on the interaction between parasite life history and host density, and the mediation of this interaction by environmental conditions.

1.4 | Do recolonizing populations have lower genetic diversity and unique allelic frequencies?

The genotypes of the limited number of individuals recolonizing secondary forests provide the foundation for the genetic diversity and composition of future generations (Figure 2). Founder effects and a genetic bottleneck would result in a recolonizing population characterized by low genetic diversity and altered allele frequencies relative

to the old-growth source population (Excoffier et al., 2009). To prevent the loss of genetic variation, connectivity between primary and secondary forest must be high enough to allow the accepted minimum of 1–10 migrants per generation (Nathan et al., 2017). In the absence of adequate gene flow, stochastic processes can create a pattern of genetic isolation by distance between secondary and old-growth forests. Genetic drift and allele surfing could alter genetic diversity and composition allowing low-frequency alleles and even deleterious mutations in the source population to accrue rapidly in the new group of individuals (Gralka et al., 2016). These negative consequences could be mitigated to a certain extent by Allee effects which are common in small populations (Fauvergue et al., 2012). In pushed waves of range expansion, Allee effects significantly modify genetic diversity on the expansion front by conserving genetic variation from the core population in the expanding range; alternatively, in pulled expansion waves, the absence of Allee effects results in the genetic diversity of the expanding population being seeded only those demographically isolated members on the expansion front (Roques et al., 2012).

Alternatively, if traits advantageous to recolonization are genetically controlled, the resulting pattern will be one of isolation-by-environment (Wang & Bradburd, 2014). Under strong natural selection, heritable, beneficial alleles should thus be disproportionately represented at the expansion front generating a pattern of spatial sorting (Phillips & Perkins, 2019). In the absence of strong gene flow and phenotypic plasticity, this spatial sorting will result in rapid phenotypic and genotypic divergence (Perkins et al., 2013). If recolonizing populations share an evolutionary history with secondary forest, however, retained traits that increase the variation upon which selection can act might increase the rate at which the genetic signature of recolonization decays (Phillips et al., 2010).

2 | DISCUSSION

Like many theoretical frameworks, the core predictions of range expansion are rooted in simplified constructs of natural systems. Nevertheless, in nature recolonization happens in complex landscapes mosaics including forest sources of different ages and secondary forests with different generative processes. Therefore, the answers to the questions described above are contingent on landscape attributes including patch configuration and degree of connectivity between old-growth forest remnants and secondary forest patches. At the community level, landscape attributes such as patch size complement other factors such as floristic composition, and forest structure as key determinants of biodiversity patterns in chronosequence studies (e.g., Acevedo-Charry & Aide, 2019; Bowen et al., 2007; Pardini et al., 2005). At the population level, larger and heterogeneous patches will be able to hold a larger population with greater genetic variability (Almeida-Gomes et al., 2016; Bowman et al., 2002). Similarly, the degree of landscape connectivity has multiple consequences for the eco-evolutionary processes driving recolonization. Connectivity determines

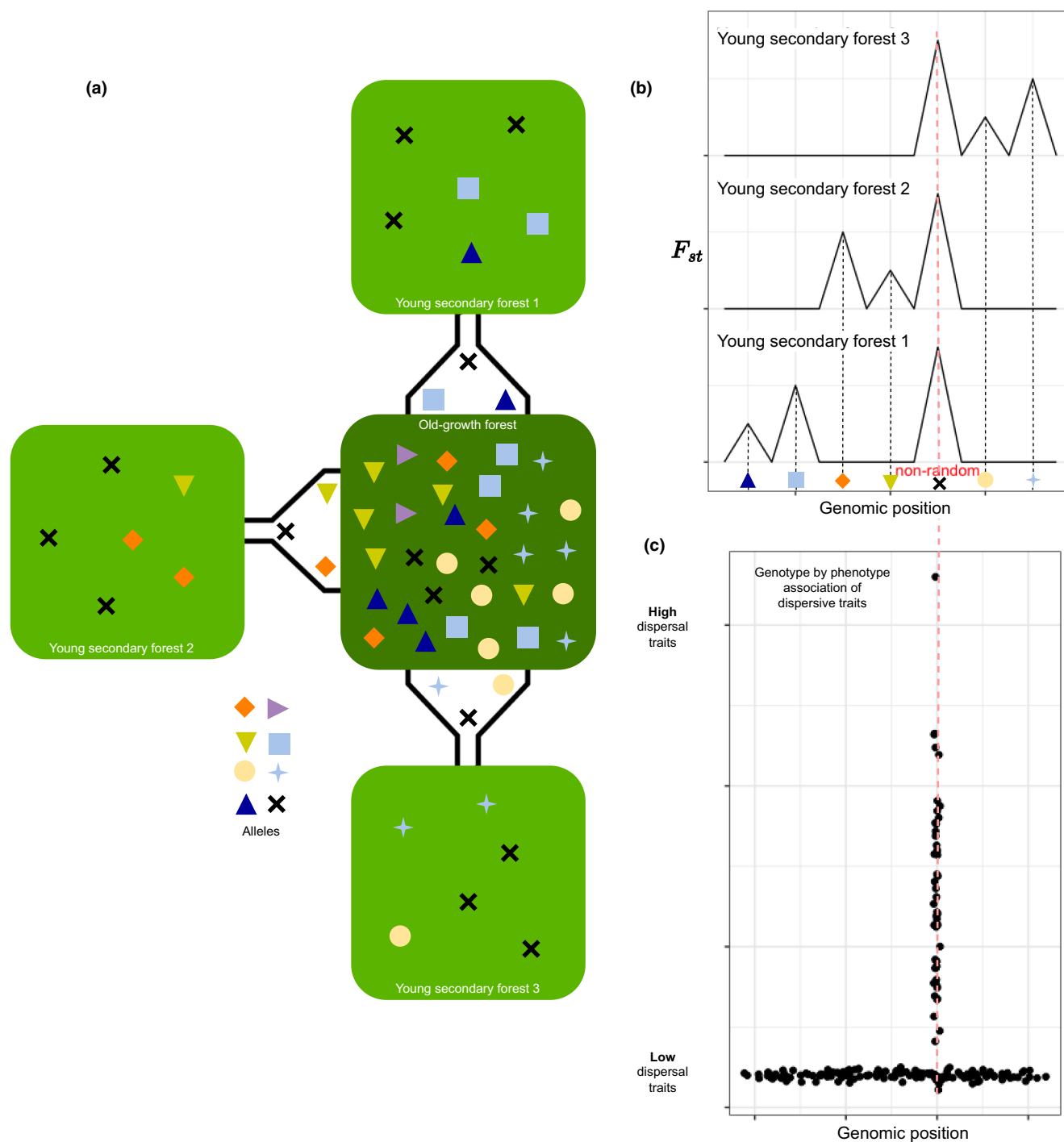


FIGURE 2 Secondary forests are hypothesized to have lower genetic diversity and unique allele frequencies when compared to old-growth forest at the early stages of recolonization. (a) In this abstract depiction, there are eight alleles present in the old-growth forest. These alleles disperse to young secondary forests with unequal probabilities. (b) One allele is overrepresented in all secondary forests (c) representing a high dispersive trait as an example. Each comparison between old-growth forests and secondary forests would generate a unique genetic pattern except for reoccurring genetically advantageous variants represented by the vertical red line overlapping (b) and (c). The potential genetic signature of selection reflecting high dispersal or adaptation to secondary forest environments is hypothesized to present a strong and consistent genetic differentiation in comparisons between old-growth and young forests.

adaptive dispersal strategies (Henriques-Silva et al., 2015). If connectivity between old-growth and young secondary forests is high dispersive traits may not be as advantageous, and adaptations to the novel conditions in secondary forests (e.g., higher temperature

tolerance) would be more relevant. This effect will be amplified if the secondary forest patch is connected to multiple large old-growth forest remnants. The high rate of movement between forest types would also decrease the amount of time where the

re-colonizing population experiences density independence and escape from natural enemies. Lastly, the duration of forest succession will also mediate these ecological processes. For instance, systems adapted to high levels of disturbance such as hurricane-prone regions or some types of dry forests may experience faster rates of succession decreasing time to initial colonization and the amount of time that individuals experience density independence (Culbertson et al., 2022).

The application of range expansion's theoretical framework to understand secondary forest recolonization does not come without its challenges. While range expansion theory has been applied to understand multiple types of expansions, most of its empirical support comes from invasive species and recent studies argue that the eco-evolutionary processes that drive invasions are fundamentally different than other types of expansions (Banks et al., 2018). First, the introduction of invasive species is often related to direct human introductions, while native species range expansion is driven by natural forest regeneration. Second, secondary forest recolonization would be highly dependent on connectivity to old-growth forest sources. Third, native species may share an evolutionary history with their colonizing sites including adaptations for environmental conditions and co-evolved enemies. If animal populations re-colonizing secondary forests follow the general predictions from range expansion theory, it will provide evidence that the theory is general and robust. If not, then it will suggest the need to modify, extend, or recast the theory.

AUTHOR CONTRIBUTIONS

MAA, CF, and RP conceived the ideas. MAA and CF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no data were created or analyzed in this study.

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