

The Paradox of Forest Fragmentation Genetics

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Abstract: *Theory predicts widespread loss of genetic diversity from drift and inbreeding in trees subjected to habitat fragmentation, yet empirical support of this theory is scarce. We argue that population genetics theory may be misapplied in light of ecological realities that, when recognized, require scrutiny of underlying evolutionary assumptions. One ecological reality is that fragment boundaries often do not represent boundaries for mating populations of trees that benefit from long-distance pollination, sometimes abetted by long-distance seed dispersal. Where fragments do not delineate populations, genetic theory of small populations does not apply. Even in spatially isolated populations, where genetic theory may eventually apply, evolutionary arguments assume that samples from fragmented populations represent trees that have had sufficient time to experience drift, inbreeding, and ultimately inbreeding depression, an unwarranted assumption where stands in fragments are living relicts of largely unrelated predisturbance populations. Genetic degradation may not be as important as ecological degradation for many decades following habitat fragmentation.*

Keywords: forest fragmentation, forest genetics, gene dispersal, inbreeding, long-distance pollination, tree genetics

La Paradoja de la Genética de la Fragmentación de Bosques

Resumen: *La teoría predice una gran pérdida de diversidad genética por deriva y endogamia de árboles sujetos a la fragmentación de hábitat; sin embargo, el soporte empírico de esta teoría es escaso. Argumentamos que la teoría de la genética de poblaciones puede ser mal aplicada a la luz de realidades ecológicas que, al ser reconocidas, requieren del escrutinio de los supuestos evolutivos subyacentes. Una realidad ecológica es que los límites de los fragmentos a menudo no representan los límites para las poblaciones de árboles que se benefician con la polinización a larga distancia, a veces favorecida por la dispersión de semillas a larga distancia. Donde los fragmentos no delimitan poblaciones, la teoría genética de las poblaciones pequeñas no aplica. Aun en poblaciones espacialmente aisladas, donde la teoría genética eventualmente puede aplicar, los argumentos evolutivos asumen que las muestras de poblaciones fragmentadas representan árboles que han tenido suficiente tiempo para experimentar deriva, endogamia y, finalmente, depresión por endogamia, una suposición que carece de base y donde los individuos de los fragmentos son relictos vivientes de poblaciones no emparentadas antes de la perturbación. La degradación genética puede no ser tan importante como la degradación ecológica durante muchas décadas después de la fragmentación del hábitat.*

Palabras Clave: dispersión de genes, endogamia, fragmentación de bosques, genética de árboles, genética forestal, polinización a larga distancia

Introduction

Accelerating forest fragmentation presents a scientific paradox because widely tested theoretical predictions

have not been borne out by empirical evidence. Classical population genetics theory predicts widespread negative genetic consequences when formerly continuous tree populations are fragmented into smaller sizes (Young

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et al. 1996; Lowe et al. 2005). Contrary to expectations, evidence of genetic doomsday for forest trees is elusive, consistent with an earlier prediction that ecological factors are likely a more imminent conservation threat than genetic degradation (Caughley 1994). We explored forest fragmentation from ecological and population genetics perspectives. We asked whether the contradiction lies in the predictions, the evidence, or the limited time scales studied by fragmentation researchers. We suggest 4 broad solutions that combine ecological and genetic perspectives to resolve an apparent paradox between clear theoretical predictions of genetic decline in fragmented forests and a dearth of empirical support.

Predicted genetic consequences of habitat fragmentation on forest trees emerge from the well-developed theory of population genetics. In effect, elimination or reduction of gene flow among fragments lowers effective population sizes for tree species remaining in fragments, where random genetic drift and chance fixation of alleles erodes genetic diversity of newly diminished populations, lowering their capacity to respond to environmental change. Furthermore, trees in small fragmented populations may experience increased selfing and biparental inbreeding among relatives, leading to inbreeding depression as recessive deleterious alleles are exposed in homozygotes. One expects diminishing genetic diversity in forest fragments, resulting in decreased progeny and reduction in overall population fitness.

Implications for conservation and management of forest trees, given the most extreme predictions of genetic theory, are profound. If loss of genetic variability and inbreeding depression indeed plague fragmented tree populations, long-term survival of many or even most species is in doubt. If, on the other hand, genetic threats are less pressing than ecological or demographic risks, a focus on genetic consequences of fragmentation represents missed opportunities to address key ecological risks (Asquith 2001). Shifting focus to environmental factors of immediate concern, and ecological factors predisposing some species or populations to genetic threats more than others, will lead to more actionable outcomes in curbing the effects of forest fragmentation.

Temperate and Tropical Forests

Habitat fragmentation is a global reality. Tree species in both tropical and temperate systems are likely to suffer if fragmentation reduces population sizes enough so that negative genetic effects come into play. Species-abundance distributions appear to make this result almost inevitable (e.g., Maina & Howe 2000). All ecological communities have skewed species-abundance distributions, with some species common, many infrequent, and most quite rare in any given area (Preston 1948; Hubbell 2001; Magurran 2004). Tropical forests are more diverse than

temperate forests, with many tree species co-occurring, most at low densities. In hyperdiverse western Amazon forests, for example, the majority of the 800–1000 tree species occur at densities of 0.1 to 1 individual/ha over tens of thousands of square kilometers (Pitman et al. 2001). A study in the Brazilian Amazon reports that the average size of isolated fragments ranges from 1.5 to 3.5 ha (Peres 2001); it follows that in “typical” fragments, most species present are represented by one to very few individuals. Hubbell and Foster (1983) demonstrate the principle in a more typical tropical forest in Central America. In a 50-ha plot of continuous old forest, 57% of 189 species (diameter at breast height of 20 cm) are represented by fewer than 16 individuals. In 2.6-ha subsets of this same plot, 86% of an average of 85 species are represented by fewer than 16 individuals, with many represented by 1–3 individuals. If these samples instead represented reproductively isolated fragments, the genetic prospects for the vast majority of tropical forest species would be dismal indeed.

Temperate forests have far fewer species, ranging from 2 to about 20 tree species (Bormann et al. 1970) occurring at densities of several to 80 or more individuals per ha (diameter at breast height of 10 cm; J. Clark et al., unpublished data). Given that mean fragment size in North America’s temperate forests ranges from 20 to over 250 ha (Heilman et al. 2002), populations of over 100 individual trees reside within most temperate forest fragments. Inherent low diversity and larger average fragment size in North American forests expose temperate trees to less potential risk of fragmentation’s negative genetic effects than tropical trees. Even without long-distance pollen and seed dispersal (hundreds to thousands of meters), most temperate trees in most places have enough conspecific neighbors to make genetic interchange likely.

Nevertheless, the potential for genetic degradation in tropical forests may be overstated. Tropical forest trees evolved in a context of low densities and large distances between conspecifics; their pollination systems necessarily accommodate long-distance pollination. Adaptation to obligate long-distance pollination may make many tropical trees more resistant to genetic isolation imposed by forest fragmentation than temperate trees. Such broad generalizations must be evaluated in light of evolution, life history, mating systems, and pollination syndromes forest-by-forest, or even species-by-species, comparisons. Such considerations will provide a more complete, albeit complex, understanding of forest fragmentation and its consequences.

Mixed Empirical Signals

Numerous researchers have tested for genetic declines in fragmented forests. They typically applied various indices of genetic diversity, estimated levels of inbreeding,

or tested for inbreeding depression with fitness measures in a comparison between trees in fragments and continuous forests. Using molecular markers, a few researchers report significantly decreased genetic diversity in at least one measure of genetic variation in at least some fragments. Examples include insect-pollinated Neotropical *Pithecellobium elegans* (Hall et al. 1996); wind-pollinated temperate European beech (*Fagus sylvatica*) (Jump & Penuelas 2006) and pedunculate oak (*Quercus robur*) (Vakkari et al. 2006); and animal-pollinated Australian white box (*Eucalyptus albens*) (Prober & Brown 1994). In contrast, others report no reduction in genetic variation in fragments, including tropical *Caryocar brasiliense* (Collevatti et al. 2001), *Carapa guianensis* (Hall et al. 1994), *Dinizia excelsa* (Dick 2001), and temperate ash (*Fraxinus excelsior*) in Europe (Bacles et al. 2005) and maple (*Acer saccharum*) in North America (Fore et al. 1992; Ballal et al. 1994). If a publication bias against reporting nonsignificant effects exists (Ghazoul 2005), loss of genetic variation in fragmented forests may be even less common than published reports indicate.

Molecular markers offer precise tools to characterize mating systems and levels of inbreeding among trees. Results of some studies consistently show higher levels of inbreeding (selfing or biparental) in forest fragments, but these are in a distinct minority. Results of 2 studies show that trees isolated after conversion of tropical forests to pastures have higher rates of selfing (Aldrich & Hamrick 1998; Dick et al. 2003). In addition to reduced genetic variation in European beech, Jump and Penuelas (2006) also report increased inbreeding in fragments. If derived from current molecular methods, levels of inbreeding may be underestimated because only successful fertilizations are assessed; inbred seeds may be aborted (Hufford & Hamrick 2003; O'Connell et al. 2006b). New methods may allow for comparison of pollen pools before and after fertilization (Matsuki et al. 2007). Nevertheless, the more common pattern appears to be extensive outcrossing and long-distance pollen movement, even among fragments (e.g., Fore et al. 1992; Dow & Ashley 1996, 1998; Bacles et al. 2005; Goto et al. 2006; Craft & Ashley 2007). Perhaps the best evidence to date is with pines, which show a mean pollen migration rate of 6.5% of at least 2 km in *Pinus flexilis* in Colorado (Schuster & Mitton 2000) and an astonishing 4.3% pollen immigration of at least 30 km for an isolated stand of *P. sylvestris* in Spain (Robledo-Arnuncio & Gil 2005). Genetic degradation of tree populations may occur in fragmented temperate and tropical landscapes, but it may be rare.

Even where inbreeding exists, negative fitness effects of inbreeding depression do not necessarily follow. Some plant species, particularly self-compatible species, are resistant to inbreeding depression, having already experienced genetic bottlenecks that eliminate most deleterious alleles (Husband & Schemske 1996). Where reproductive output is a proxy for lifetime fitness, results

remain mixed. Results of several studies show significantly lower output from trees in fragments compared with those in continuous forest in some tropical and subtropical (Nason & Hamrick 1997; Cunningham 2000; Ghazoul & McLeish 2001) and temperate (O'Connell et al. 2006a) species. Results of as many studies show higher reproductive output in trees in fragmented or disturbed tropical or subtropical habitats (Aizen & Feinsinger 1994; Aldrich & Hamrick 1998; Dick 2001; Boshier et al. 2004). Results of other studies in tropical habitats show no significant differences (Aizen & Feinsinger 1994; Aldrich & Hamrick 1998; Boshier et al. 2004). Progeny fitness is a better measure of inbreeding depression, but data are scarce. In one example from the tropical tree *Spondias mombin*, progeny fitness in fragments is lower than in forests (Nason & Hamrick 1997) but gene flow is actually higher in fragmented forests. Environmental, rather than genetic, factors probably account for progeny fitness differences in this *Spondias* population. The general message from existing evidence is that there is no clear signal that genetic inbreeding consistently affects fecundity or progeny fitness.

Resolving the Paradox by Examining the Assumptions

Why has it been difficult to find clear genetic signals of forest fragmentation? We suggest that incorporation of ecological perspectives and reexamination of 4 key assumptions offers clues: (1) fragment edges delimit populations, (2) genetic declines manifest quickly enough to detect, (3) tree species respond similarly to fragmentation, and (4) genetic declines supersede ecological consequences.

Fragment Edges Delimit Populations

One key assumption is that trees in forest fragments are reproductively isolated from conspecifics elsewhere. Application of genetic theory is appropriate if fragments delineate much smaller populations than once existed in continuous forests. This occurs if forest-fragment edges circumscribe movement of pollen and seeds of trees residing in that fragment (Fig. 1, line 2). The supposition of circumscribed subpopulations underlies the application of population genetics theory of small populations to predict a steady decline of genetics-related fitness over time. A wealth of evidence now calls into question the assumption that dispersal of pollen and seed stops, or at least declines dramatically, at fragment edges for many tree species.

The application of molecular markers in pollen-dispersal studies in which paternity assignment was used provides a more detailed picture of pollination patterns than was available with more traditional approaches.

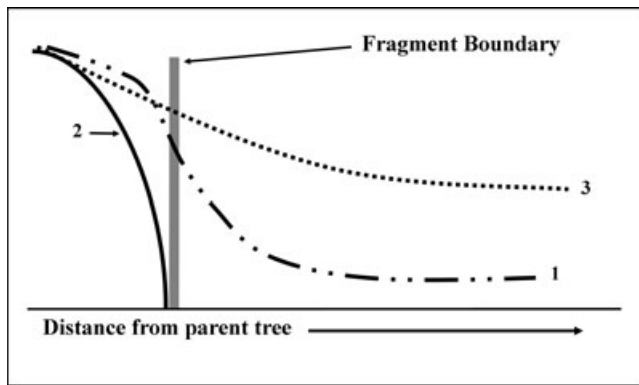


Figure 1. Schematic representation of seed and pollen dispersal curves and potential impacts of fragmentation. Line 1 represents traditional views of a leptokurtic thin-tailed distribution without fragmentation or when the fragment boundary does not affect dispersal. In line 2, the fragment boundary limits or truncates dispersal. In line 3, the fragment boundary enhances dispersal distances, resulting in a fat-tailed distribution.

Such studies reveal many examples of long-distance pollen movement, often revealing a surprisingly weak relationship between pollination and distance between trees. Numerous studies call into question the dogma that most pollination occurs among nearest neighbors and that long-distance pollination is either rare or nonexistent. A study of the Neotropical canopy tree *Pithecellobium elegans* revealed pollination distances of up to 350 m, with an average pollination distance of 142 m (Chase et al. 1996). *P. elegans* is pollinated by hawkmoths (*Manduca*); such long-distance pollination may be expected for strong fliers such as birds, bats, hawkmoths, and large bees. Similarly, in continuous forest on Barro Colorado Island, Panama, the animal-pollinated and dispersed tree *Simarouba amara* shows mean pollen and seed movement of 345 and 392 m, respectively, with measured extremes approaching or reaching 1000 m (Hardesty et al. 2006). Intriguingly *Simarouba* actually recruits offspring near parents far less than expected, indicating that normal pollen and seed movement are greater than anticipated and that neighbors are often not relatives.

In addition to such examples of substantial normal gene flow, remarkable long-distance connectivity occurs. Fig (*Ficus*) trees, for example, are pollinated by minute fig wasps that routinely carry pollen several kilometers through tropical rainforest (Nason et al. 1998). In another extreme example, 2 juvenile heart-of-palm trees (*Euterpe edulis*) had a parent 22 km away (Gaiotto et al. 2003). Studies of wind-pollinated temperate trees also reveal pollination occurring at surprisingly long distances. Immigration of pine pollen from distances of 2 to 30 km indicate far more extreme possibilities comparable to or

exceeding extremes for animal-pollinated tropical trees (Schuster & Mitton 2000; Robledo-Arnuncio & Gil 2005). Most researchers underestimate pollination distances because paternity-assignment approaches only include sampled potential fathers in a circumscribed study area, underscoring the value of pine studies where focal stands are far from other sources of conspecific pollen.

Occasional long-distance pollination events are not likely to entirely offset the genetic consequences of fragmentation. But in many cases, long-distance pollination is not rare at all, with pollen coming from outside a stand or fragment accounting for a large proportion of pollinations. In the Neotropical tree *Dicorynia gianensis*, 62% of pollen came from outside the study stand (Latouche-Halle et al. 2004). For Neotropical *Swietenia humilis*, gene flow into isolated fragments accounted for 38–68% of pollinations at distances >1 km (White et al. 2002). In the Neotropical dry forest *Enterolobium cyclocarpum*, between 61 and 100% of pollen donors were located outside the studied fragment (Apsit et al. 2001). Studies of wind-pollinated trees show similar results. In oaks pollen from outside study stands, even isolated stands, accounts for the majority of pollinations (Dow & Ashley 1998; Streiff et al. 1999; Nakanishi et al. 2004). Interestingly, pollen-dispersal curves for some species in fragments actually have broader tails than their counterparts in continuous forests (Fig. 1, line 3) (Young & Merriam 1994; Nason & Hamrick 1997). Moderate and quite ordinary pollen dispersal of a few hundred meters is sufficient to bind together many apparently isolated stands of trees in archipelagoes of fragments.

Seed dispersal can also be an important component of gene flow because a diploid seed carries twice the genetic complement as a pollen grain and is far more likely to contribute to the next generation. In tropical forests fragment boundaries may reflect approximate limits to seed dispersal by small arboreal, terrestrial, or weak-flying dispersal agents that do not cross open land (e.g., Cordeiro & Howe 2001; Cordeiro & Howe 2003). Seed traps in open fields in Mexican and Asian habitats show limited dissemination of wind-dispersed species away from forest edges (most such tropical seeds are >0.5 g) and very limited dispersal of large animal-dispersed seeds into the open spaces themselves (Martinez-Garza & Gonzalez-Montagut 1999; Ingle 2003). Nevertheless, seed dispersal across a fragmented landscape may be common for small wind-dispersed seeds (Jones et al. 2005; Bacles et al. 2006; Gonzalez-Martinez et al. 2006; Sato et al. 2006) or for seeds dispersed by birds, bats, or ground mammals consistently flying or walking long distances to feeding or roosting sites (e.g., Daily et al. 2001; Estrada & Coates-Estrada 2002; Bacles et al. 2004). With vagile dispersal vectors, such as large birds (>500 g), large bats (>150 g), or terrestrial birds or mammals (>2 kg), trees may have “fat” dispersal tails (Clark et al. 1999) (Fig. 1, line 3) or multimodal distributions determined by perch sites,

seed caches, and feeding trees (Jordano & Godoy 2002; see Holbrook et al. (2002) and Westcott et al. (2005) for seed dispersal by birds 1–60 kg). Data on such cases are sparse, but indicate that gene flow by seed dispersal among fragments depends on the vector, the tree, and the fragmentation matrix.

The evidence at hand indicates that, from the perspective of mating trees, fragments frequently do not define populations. As a result, extreme negative genetic effects of small population size are rarely realized. We are forced to conclude that for some trees, the actual breeding population may include many fragments and forest remnants in a large landscape.

Genetic Declines Manifest Quickly

A second assumption is that genetic consequences of forest fragmentation will appear within a generation or 2 after fragmentation, and therefore can be measured by sampling contemporary tree cohorts. The reality is that even if fragmentation limits pollen or seed dispersal among fragments, trees in most human-created fragments have not had enough time to show genetic fragmentation effects. Most forest fragmentation is recent (20–200 years), and trees are generally long-lived (over 50 years). Adult trees sampled for most published fragmentation genetic studies represent remnants from the prefragmentation past or are, at most, 1 or 2 generations removed from isolation. No loss of genetic diversity exists where adult trees remain from continuous forests. For postfragmentation generations to show quantitative genetic diversity loss or clear inbreeding effects in a generation or two, populations would have to be very small and isolated. Genetic signals of fragmentation likely require several generations to appear, perhaps amounting to hundreds of years in the case of long-lived tree species.

Inbreeding, genetic isolation, and genetic bottlenecks were detected in historically fragmented (>600 years) populations of *F. sylvatica*, a wind-pollinated temperate tree (Jump & Penuelas 2006). In contrast, bur oaks (*Q. macrocarpa*) have existed in scattered savanna groves for over 5000 years, yet show no evidence of genetic bottlenecks or isolation (Craft & Ashley 2007). Thus trees with similar pollination modes may not respond to fragmentation in similar ways, but genetic declines are certainly not the only risk factor to investigate in fragmented landscapes.

Forest Tree Species Have Similar Responses to Fragmentation

Expectations for negative genetic effects are often applied across tree taxa that differ widely in mating system, pollination and dispersal biology, and other ecological factors. Fragments and intervening matrices differ markedly, and not all tree species respond to fragmentation in similar ways. For any species an array of interacting factors determines whether and how fragment edges

interrupt gene flow or how a population responds over multiple generations when population size drops dramatically. Far too few studies take potential fragmentation modifiers into account.

A tree's mating system influences how fragmentation affects successful pollination. Species with self-incompatibility systems may be able to maximize their offspring's genetic diversity beyond the predictions of genetic theory. Self-incompatible trees may better avoid inbreeding depression over the short term because only biparental inbreeding, not selfing, is possible. Alternatively, self-incompatible species may be more susceptible to the deleterious effects of biparental inbreeding because purging of deleterious alleles through selfing is not part of their evolutionary histories (e.g., Husband & Schemske 1996; Latouche-Halle et al. 2004). Outcomes depend on the species, its current circumstances, and its history.

Other aspects of tree breeding systems have implications for fragmentation. Because successful reproduction in dioecious species requires both male and female plants, effective population size is roughly half that of hermaphroditic species, increasing the risk of severe fragmentation impacts. Even in such cases, however, normal pollen and seed dispersal may be sufficient to preclude genetic isolation on a local scale. At least one temperate, dioecious wind-pollinated tree (*Cercidiphyllum japonicum*) naturally grows in low densities, is readily pollinated (Sato et al. 2006), and, because of long-distance pollination and seed dispersal by wind, may be quite resilient to fragmentation. Although populations differ genetically across Japan, fine-scale genetic structure cannot be detected by microsatellites within one intensively studied 20-ha study site. Even where genetic structure is expected, it is elusive.

Ecological circumstances sometimes compensate for losses of pollination or dispersal agents. For *Calathea ovadenensis* in Mexican rainforest, when the most effective bee pollinator (*Rathymus*) is absent, most pollination is effected by more common taxa (e.g., *Euglossa*, *Eulaema*) that are less efficient per visit but have many more visits (Horvitz & Schemske 1990). Compensation appears to occur for some bird-pollinated plants in fragmented forests; most pollinators drop out, but 1 or 2 species released from competition are likely effective pollinators and mediators of gene flow among fragments (Bond 1994). For instance, variation in pollinators between years has little effect on the overall pollen dispersal distance in the tropical tree *Dipterocarpus tempehes* (Kenta et al. 2004). Loss of native bees in pasture and fragmented habitat in the central Amazon do not negatively affect pollination of the forest tree *D. excelsa* because exotic Africanized bees are more effective pollinators and mediators of gene flow than native bees (Dick et al. 2003). Similar compensation is possible in seed-dispersal systems. On tropical Pacific islands, loss of seed-dispersing pigeons is

compensated by increases in fruit-bat populations (McConkey & Drake 2002). Much as Caughley (1994) warned years ago, the clarity of predictions made on the basis of genetic theory of small populations must be tempered by an understanding of how species-specific ecological realities violate simple assumptions underlying the theory.

Genetic Declines Supersede Ecological Consequences

If long-distance pollen dispersal is actually common and borders of populations of forest trees typically extend beyond fragment boundaries, failure due to genetic isolation may not be as immediate a concern as failure for ecological reasons. Forest fragments may not be reproductively isolated or suffer losses of genetic diversity, but may instead experience quantitative pollen limitation (O'Connell et al. 2006a). This could explain the findings of Knapp et al. (2001): acorn production is correlated with the number of nearby flowering cohorts for *Q. douglasii*. Ample genetic mixing from long-distance pollen movement is common in oaks (Dow & Ashley 1996, 1998; Streiff et al. 1999; Craft & Ashley 2007), but lower fecundity could reflect sparser pollen volumes. Quantitative reduction in pollen availability may be exacerbated in the tropics, where habitat loss may, in the absence of ecological compensation, reduce the number, diversity, or efficiency of pollinators (Didham et al. 1996). For instance, fewer bats visit balsa trees (*Ceiba grandiflora*) in forest fragments in southern Mexico and less pollen is deposited, which results in lower fruit set (Quesada et al. 2004). Bats are capable of long-distance flight, but the logistics of finding scattered trees in a fragmented landscape reduce visitation and effectiveness. Even if genetic variation among offspring of balsa trees is indistinguishable in fragments and continuous forest, a 40% reduction in fruit set from pollen limitation is a demographic risk for this tree in fragments.

Similarly, dispersal limitation might easily result in recruitment limitation, which could be misidentified as a consequence of genetic effects. In Tanzanian forests the most important avian seed dispersers of *Leptonychia usambarensis* are 2 species of greenbuls (*Andropadus*), which occur in lower numbers and eat fewer fruits in fragments than in continuous forest (Cordeiro & Howe 2003). Evidence for inbreeding is lacking, but a 75% reduction in seed dispersal poses a severe threat for recruitment. Indeed, densities of endemic animal-dispersed trees are lower in fragments than densities of other trees (Cordeiro & Howe 2001). We suspect that quantitative reductions in effective pollination and dispersal, rather than losses of genetic variability, account for most depressed recruitment of trees in forest fragments.

Conclusions

The population genetics of forest fragmentation is a thornier issue than simple application of population ge-

netics theory suggests. It is not safe to assume that fragments contain isolated tree populations to which genetic theory of small populations applies. Theory might apply well to some species, but not at all to many or even most others. It is not safe to ignore the myriad ecological factors altered by fragmentation, what we call fragmentation modifiers, which affect the ecology, demography, and reproductive biology of trees residing in fragments. Pollination and seed dispersal patterns are usually poorly understood in either intact or fragmented forests. Current evidence suggests that long-distance pollination and sometimes seed dispersal prevent genetic isolation in many species. Ecological compensation by members of pollinator or dispersal guilds released from competition, or introduced pollinators and dispersers, may prevent genetic isolation in fragmented stands that otherwise might show it in time. At the present state of knowledge there is no justification for expecting universally rapid loss of genetic variability in forest fragment stands or for proclaiming genetic processes inconsequential. Neither the ecological nor genetic issues have been addressed broadly with respect to each other.

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