

FORUM

Habitat fragmentation and plant populations: is what we know demographically irrelevant?

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Abstract: Habitat fragmentation is considered a leading cause of plant extinction, and matrix models provide a powerful set of tools with which to identifying mechanisms that influence population declines. We surveyed the ecological literature to determine what components of plant demography have been studied in fragmented habitats, and determined the elasticity values of the vital rates influenced by these components. We found that there is a major disparity between the ecological processes and stages of life history with large demographic impacts and the focus of empirical research on plants in fragmented habitats. While the growth and survivorship of large, established individuals have the highest elasticity values, the focus of empirical research has been on components of reproduction and seedling dynamics. We argue that elucidating the demographic mechanisms underlying population declines in fragmented habitats, and developing strategies for mitigating these declines, will be challenging without a greater focus on understanding how fragmentation alters adult plant growth and survivorship.

Keywords: Demography; Elasticity analyses; Fertility; Lambda; Matrix models; Pollination; Seed banks; Seedling recruitment; Vital rates.

Introduction

Habitat fragmentation was first identified as a threat to the integrity of ecosystems over 20 years ago (Harris 1984; Wilcove et al. 1986), and understanding the consequences of fragmentation has since emerged as one of the principal areas of research in conservation biology. Hundreds of studies

conducted in diverse biomes have documented myriad and pervasive ecological changes associated with fragmentation of formerly contiguous landscapes. One of the most widely observed consequences of fragmentation is a reduced number of species in remnants, particularly when compared to similarly sized areas of continuous habitat (reviewed in Laurance & Bierregaard 1997; Harrison & Bruna 1999; Debinski & Holt 2000; Young & Clarke 2000). Although numerous factors could account for these differences, they are often attributed to the local extinction of populations in fragments following their isolation (e.g. Fischer & Stocklin 1997; Bolger et al. 2000; Tabarelli et al. 2004).

The process by which a population declines to extinction is demographic. Consequently, considerable empirical attention has focused on documenting how factors believed to influence the growth rate of populations are modified in fragmented areas (reviewed in Hobbs & Yates 2003). Both experimental and observational studies have demonstrated that the biotic and abiotic changes associated with fragmentation can dramatically alter fertility, growth, and survivorship. For example, the mortality rates of Amazonian trees are often higher near forest edges than in forest interiors (Laurance et al. 1998b), and surrogates of fertility such as fruit set (Cunningham 2000a) and seedling abundance (Benitez-Malvido 1998) are often lower in habitat fragments. Although the observed changes in these demographic vital rates are often put forward as primary mechanisms underlying extinction from fragments (Cardoso da Silva & Tabarelli 2000; Bruna 2002), few studies have simultaneously evaluated how fragmentation influences multiple

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demographic processes in isolated populations. We therefore know little regarding the relative importance of different vital rates as drivers of decline (but see Jules 1998; Bruna 2003).

Matrix models (Leslie 1945; Lefkovich 1965) are an important tool with which ecologists analyze the demography and dynamics of plant and animal populations. One of the most powerful applications of matrix models is their ability to predict how changes in individual vital rates would influence the deterministic and stochastic rates of population growth (i.e., λ and λ_s , respectively; reviewed in Caswell 2001; Morris & Doak 2002). Of particular interest to conservation biologists has been the *elasticity* of vital rates – the proportional change in λ for a given change in a vital rate (de Kroon et al. 2000). Although a population's growth rate is shaped by the interaction of all vital rates, elasticity analyses have shown that changes in some vital rates could have a proportionately greater impact on λ than others (Kalisz & McPeck 1992; Morris & Doak 2005). Vital rates with high elasticities could therefore indicate specific targets for conservation action, since even small changes in those vital rates could lead to proportionally large increases in λ (but see Mills et al. 1999; de Kroon et al. 2000). Identifying vital rates with high elasticities, and how they and the interactions that influence them have changed in habitat fragments, could be an important first step in ameliorating declines in abundance (Bruna 2003).

We surveyed the literature from two well established but disparate fields – plant demography and the ecological effects of habitat fragmentation – to address two questions. First, what components of demography have been studied in fragmented habitats? Second, what are the elasticity values of the vital rates influenced by these components? Our objective here is not to determine if fragmentation influences certain vital rates more than others, nor to determine the magnitude of these effects; instead, we wish to assess the potential demographic impact of the ecological interactions studied by conservation biologists working in fragmented landscapes. We focused our efforts exclusively on plants because there is both a rich demographic literature and an extensive body of empirical research investigating the effects of habitat fragmentation.

Literature Survey and Demographic Analyses

To identify studies that investigated the effects of habitat fragmentation on components of plant demography, we conducted searches of all papers

listed in the Web of Science through May 2005. These searches were conducted by combining strings targeting studies of habitat fragmentation (i.e., “habitat fragmen*”, “forest fragmen*”, “fragmen* habitat”) with those focusing on studies of plant demography (i.e., “plant”, “population dynamics”, “seed*”, “seed predation”, “fertility”, “reproduction”, “germination”, “growth”, “mortality”, “seed set”, “fruit set”, “dispersal”, “demograph*”). For each study, we then used the Web of Science's “References” and “Times Cited” functions to identify additional relevant studies that we might have missed using our search strings. Finally, we surveyed all papers cited in two recent syntheses of how habitat fragmentation influences plants (Laurance et al. 2002; Hobbs & Yates 2003) as well as our own personal libraries of fragmentation-related literature.

For each of the resulting studies, we identified which ecological process the authors were investigating (e.g., adult survivorship, pollination, seed dormancy, fruit production), and then assigned them to the appropriate demographic transition in a generic plant life-cycle graph (Fig. 1a). Studies that considered multiple ecological processes (e.g., Jules 1998) were assigned to all appropriate transitions. When studies evaluated the effects of fragmentation on multiple plant species, each species was counted separately. We also recorded the life-history strategy of each species (e.g., shrub, tree, perennial herb) and the habitat type in which the studies were conducted.

We conducted a similar review to compare the elasticity values for each demographic stage and transition shown in Fig. 1a. During May 2005, we searched the Web of Science using the following search strings: “plant* and matrix model”, “plant and population model”, “plant and demograph*”. From the resulting list of studies, we identified and further analyzed only those in which the authors included a transition matrix and calculated the elasticity values of the matrix elements. For each species' elasticity matrix we identified the highest elasticity value and determined what life-history stage it was associated with using the following broad categories: seedling, small/intermediate-sized plant, or large/adult plant). We also summed all the elasticity values for transition elements representing growth (G), stasis (S), regression (R), and fertility (F). Finally, we again recorded the growth form and life-history strategy of each species, as well as the habitat type in which each study was conducted. Note that the transition elements whose elasticities we calculated are themselves composed of “lower-level” vital rates (Morris & Doak 2002). However, we conducted our analyses using

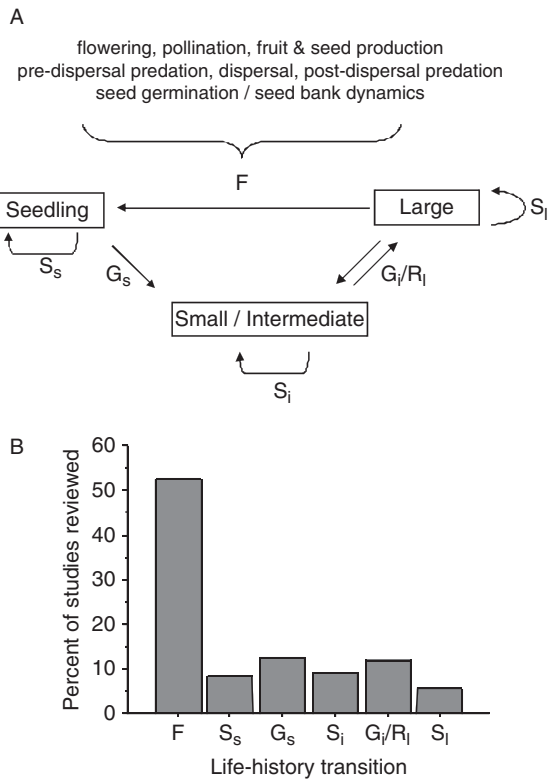


Fig. 1. (a) Generic life-cycle graph describing plant life history. Arrows represent different components of demography, including fertility (F), seedling stasis in the seedling class (S_s), growth of seedlings into larger size classes (G_s), the stasis of “small/intermediate” plants in that size class (S_i), the growth of “small/intermediate” plants or regression of larger plants into the small/intermediate category (G_s/R_i), and the survival and stasis of large plants (S_l). Note that the fertility term includes all processes from flowering through seed germination, which is typical in many matrix models. (b) Percentage of N = 107 empirical studies that evaluated the effect of fragmentation on different components of plant demography shown in (a).

transition elements rather than lower-level vital rates to simplify the comparison with experimental studies and because, in some cases, it was impossible to calculate lower-level vital rates using the data presented in the paper.

We identified 107 studies that investigated the effects of habitat fragmentation on ecological interactions or other factors that influence demographic vital rates (Appendix S1; see Supporting Information section). Most of these studies focused on a single plant species (Jennersten 1988; Gigord et al. 1999), although a number of studies investigated > 10 species simultaneously (Laurance et al. 1998b; Hewitt & Kellman 2004). Most of these studies used trees and palms with a tree-like growth habit

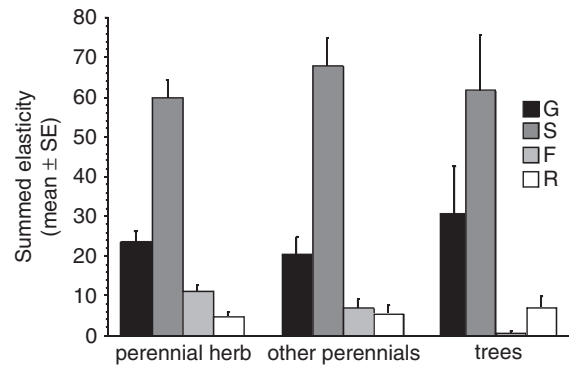


Fig. 2. Mean summed elasticities (± 1 SE) for transition elements representing growth (G), regression (R), stasis (S), and fertility (F), based on N = 42 species with three most common life-history strategies recorded in our survey.

(39.8%) or perennial herbs (35.2%) as model systems. The remaining studies were conducted on shrubs, epiphytes, and other perennial plants (11.1%), combinations of perennials, trees, and other species (8.3%), artificial seedlings (2.8%), and annual species (1.9%). Although a variety of ecosystems were represented, tropical wet forests and temperate forests were the predominant habitats in which research was carried out (31.5% and 25%, respectively), followed by tropical dry forests (17.6%), grasslands (14.8%), and fens/meadows/wetlands (11.1%). Irrespective of ecosystem or plant life history, 52.4% of studies evaluated the effect of fragmentation on processes related to plant fertility and recruitment, such as flowering, pollination, fruit production, seed germination, and seed bank dynamics (Fig. 1b). An additional 20.9% investigated the effects of fragmentation, seedling survivorship, and growth (Fig. 1b). Only 26.7% of studies evaluated the growth or survivorship of plants that were beyond the seedling stage, with few studies (e.g., Jules 1998; Laurance et al. 1998b; Laurance et al. 2000; Bruna et al. 2002; Bruna 2003) explicitly focusing on advanced-stage classes such as “adults”, “reproductive”, or “large” individuals.

Our analyses of elasticity patterns (Figs. 2 and 3) are based on 34 published studies using 42 species (Appendix S2; see Supporting Information section). A majority of the demographic studies focused on perennial herbs (52.4%), with the remainder investigating cacti, shrubs, or other perennials (33.3%) and trees (14.3%). Tropical wet forests, temperate forests, and grasslands were the most common habitats studied (23.8% each), followed by fens/meadows/wetlands (16.7%), and arid environments (9.5%). A single study was conducted in tropical dry forests (2.4%).

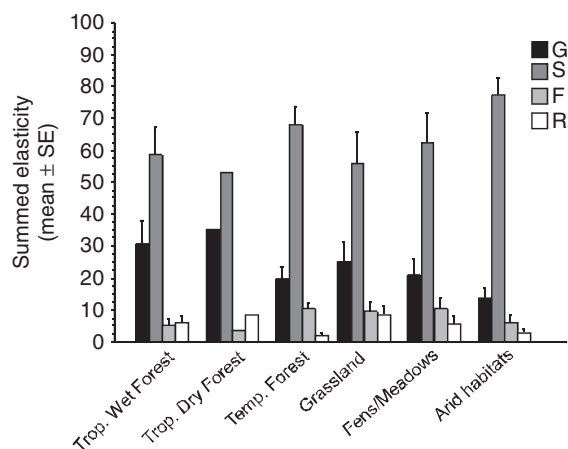


Fig. 3. Mean summed elasticities (± 1 SE) for transition elements representing growth (G), regression (R), stasis (S), and fertility (F), based on $N = 42$ species from the six most common habitat types recorded in our survey.

The transitions associated with seedling stages had the highest elasticity values in fewer than 5% of the species studied. In contrast, the term with the highest elasticity belonged to “small/intermediate” or “large” plants in 45.2% and 50% of the species, respectively. When summing the elasticities of matrix elements representing different demographic events – growth, stasis, regression, and fertility – we found the highest summed elasticities were for transition elements representing stasis (average summed elasticity of stasis terms = $62.8\% \pm 3.8$ SE) and growth (average summed elasticity of growth terms = $23.5\% \pm 2.6$ SE). Fertility and regression had the lowest elasticity values (average summed elasticity of fertility terms = $8.2\% \pm 1.2$ SE; average summed elasticity of regression terms = $5.3\% \pm 1.0$ SE).

What We Need to Know Versus What We Study

Because declines in recruitment are presumed to underlie plant extinctions in fragmented habitats (e.g., Bond 1995; Cardoso da Silva & Tabarelli 2000; Zartman & Shaw 2006b), ecologists investigating the consequences of fragmentation for plants have focused their attention on pollination, fruit and seed production, and seedling dynamics (Hobbs & Yates 2003, this study). However, elasticity analyses have generally found that the greatest proportional changes in λ would result from changes in growth and survivorship rates, especially of larger or reproductive plants (Pinerio et al. 1984; Horvitz & Schemske 1995; Olmsted & Alvarez-Buylla 1995).

This result is strikingly consistent for species from a broad range of life-history strategies (Fig. 2) and ecosystems (Fig. 3). Our results therefore suggest that there is an important and general disparity between the ecological processes and stages of life history whose manipulation in a conservation setting could have large impacts on population growth rates (i.e., stasis and growth of adults) and those that have been the focus of empirical research on plants in fragmented habitats (i.e., reproduction and seedling dynamics).

The demographic importance of individuals in the largest stage classes to populations of perennial plants is widely recognized (e.g., Horvitz & Schemske 1995; Bruna 2003). However, we found few studies that measured the growth and survival of these individuals in fragmented landscapes (Chen et al. 1992; Laurance et al. 1998a; McDonald & Urban 2004; e.g., Bach et al. 2005), and most of these studies were carried out on trees at Brazil’s Biological Dynamics of Forest Fragments Project (reviewed in Laurance et al. 2002). Furthermore, studies that simultaneously track individuals in multiple size or stage classes are exceedingly rare. In fact, we identified only three systems in which data had been concurrently collected on juvenile and adult stages (Jules 1998; Jules & Rathcke 1999; Bruna 2003; Bach et al. 2005). This paucity of demographic data clearly makes it difficult to evaluate the precise mechanisms responsible for changes in plant abundance in fragmented landscapes. Indeed, we identified only two studies that used matrix models to analyze the consequences of habitat fragmentation for plant demography (Bruna 2003; Bruna & Oli 2005).

As expected, these studies found results comparable to demographic studies conducted in non-fragmented systems – survivorship and growth of larger individuals have much higher elasticity values than terms related to plant fertility (see also Zartman & Nascimento 2006a for examples of more recent studies using alternative modeling methods; Zartman & Shaw 2006b). Understanding the extent to which the results observed in this study can be generalized to other life-history strategies will require considerably expanding ongoing data collection efforts. For instance, we found relatively few studies on annual herbs – a group for which the persistence in fragmented habitats might strongly depend on patterns of reproduction and the dynamics of seed banks (Pake & Venable 1996). The same is true for generalizing to habitat types other than the forest ecosystems that have been most commonly studied. For instance, grasslands are

globally widespread, species-rich, and highly fragmented (Klink & Machado 2005), but studies focusing explicitly on the consequences of fragmentation for plant populations in these biomes remain notably underrepresented in the literature.

Given the demographic importance of adult plant growth and survivorship, why is our understanding of these life-history processes in fragmented habitats so limited? Put another way, why have we devoted so much attention to understanding how fragmentation influences the early stages of the life cycle but so little to the impact on later stages? Early stages of plant demography such as seedling and sapling stages are readily amenable to experimental manipulation and can often be studied over shorter temporal scales. The same is true of plant reproduction and seed predation, both of which have been well studied in fragmented systems (e.g., Aizen & Feinsinger 1994; Santos & Telleria 1997; Cunningham 2000b; Dick 2002). However, assessing the growth and survivorship of long-lived plant species often requires observational studies of long duration, and these studies can be difficult to implement, administer, and support financially. Furthermore, larger shrubs and trees are rarely amenable to transplanting and other types of experimental manipulation, without which it can be difficult to distinguish among the myriad environmental changes associated with fragmentation that are responsible for changes in vital rates. Despite the challenges associated with such studies, however, we argue that long-term data collection remains the best way to quantify plant demography, and often provides unexpected insights (Laurance et al. 2006). Fortunately, increasingly sophisticated mathematical (Doak & Morris 1999; Doak et al. 2005; Gross et al. 2006) and empirical techniques (Chambers et al. 1998; Wang & Smith 2002; Vieira et al. 2005) provide complementary ways to investigate rarely explored demographic stages and ecological processes. Coupled with funding agencies and other institutions who are aware of the critical need for long-term data (Morris et al. 1999; NSF 2005), the creative use of emerging model systems (e.g., Zartman & Shaw 2006b), and the potential for experiments on juvenile stage classes to inform patterns of adult demography and distribution (Engelbrecht et al. 2007), will allow for increased opportunities to collect these critical but often overlooked demographic data.

Two important caveats to our conclusions merit further consideration. First, most studies of plant demography tend to be of limited temporal duration. The elasticity structure of populations will

undoubtedly change as the duration of the study increases, particularly for long-lived species or those found in variable environments. The same may be true of disturbance-dependent species or those with episodic recruitment – failure to include years of exceptional reproduction may cause the demographic importance of fertility-related terms to be underestimated. Second, elasticity analyses require careful interpretation (de Kroon et al. 2000; Caswell 2001), and their use as a means by which to inform conservation action requires caution (Mills et al. 1999). A useful complement to elasticity analyses and other “prospective” methods is the “retrospective” method known as Life Table Response Experiments (LTRE), which decompose observed differences in λ into the actual contributions from individual demographic variables (Caswell 1989; Caswell 2000). To our knowledge, only one study has used LTRE to evaluate plant demography in habitat fragments (Bruna & Oli 2005), making it difficult to ascertain if retrospective and prospective analyses yield similar results regarding the relative demographic contribution of different life-history stages. As these analyses become more prevalent, they may provide novel insights into demography of plants in fragmented landscapes.

It is important to emphasize that we are by no means advocating that we study how later demographic stages are altered in fragments in lieu of understanding plant reproduction, seed dispersal, or seedling dynamics. Indeed, simulation studies have suggested that despite the generally low elasticity values associated with plant recruitment, dramatic increases in reproduction can increase the growth rate of populations (Bruna 2003). In addition, transition matrices encapsulate only local population dynamics; understanding persistence at regional scales requires understanding the relative importance of local seed production and dispersal among populations. Finally, long-term population viability is also influenced by the maintenance of genetic diversity, which is directly related to the ecology of pollination, seed dispersal, and demography (reviewed in Young & Clarke 2000). However, we hope the results of our review encourage researchers interested in exploring the consequences of fragmentation for plant population viability to place their work in a broader demographic context, and more carefully consider the relative impacts of changes in different vital rates. Doing so will greatly enhance our ability to elucidate the precise demographic mechanisms underlying population declines, and aid in the development of strategies for mitigating them.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Studies evaluating the effects of habitat fragmentation on components of plant demography included in our review.

Appendix S2. Studies using matrix models and elasticity analyses to investigate plant demography included in our review.

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