Oikos 121: 161–170, 2012
doi: 10.1111/j.1600-0706.2011.20273.x

Subject Editor: Christopher Lortie. Accepted 9 September 2011

Rethinking the conceptual foundations of habitat fragmentation research

Raphael K. Didham, Valerie Kapos and Robert M. Ewers

R. K. Didham, (raphael.didham@uwa.edu.au), School of Animal Biology, The Univ. of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia, and CSIRO Ecosystem Sciences, Centre for Environment and Life Sciences, Underwood Ave, Floreat, WA 6014, Australia. – V. Kapos, UN Environmental Programme World Conservation Monitoring Centre (UNEP-WCMC), 219 Huntingdon Road, Cambridge, CB3 0DL, UK, and Dept of Zoology, Univ. of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK. – R. M. Ewers, Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY, UK.

The conceptual foundations of habitat fragmentation research have not kept pace with empirical advances in our understanding of species responses to landscape change, nor with theoretical advances in the wider disciplines of ecology. There is now real debate whether explicit recognition of 'habitat fragmentation' as an over-arching conceptual domain will stimulate or hinder further progress toward understanding and mitigating the effects of landscape change. In this paper, we critically challenge the conceptual foundations of the discipline, and attempt to derive an integrated perspective on the best way to advance mechanistic understanding of fragmentation processes. We depict the inherent assumptions underlying the discipline as a 'conceptual phase space' of contrasting false dichotomies in fragmentation 'problem space'. In our opinion, the key determinant of whether 'habitat fragmentation' can remain a cohesive framework lies in the concept of 'interdependence': 1) interdependence of landscape effects on species and 2) interdependence of species responses to landscape change. If there is non-trivial interdependence among the various sub-components of habitat fragmentation, or non-trivial interdependence among species responses to landscape change, then there will be real heuristic value in 'habitat fragmentation' as a single conceptual domain. At present, the current paradigms entrenched in the fragmentation literature are implicitly founded on strict independence of landscape effects (e.g. the debate about the independent effects of habitat loss versus fragmentation per se) and strict independence of species responses (e.g. the individualistic species response models underpinning landscape continuum models), despite compelling evidence for interdependence in both effects and responses to fragmentation. We discuss how strong 'interdependence' of effects and responses challenges us to rethink long-held views, and re-cast the conceptual foundations of habitat fragmentation in terms of spatial context-dependence in the effects of multiple interacting spatial components of fragmentation, and community context-dependence in the responses of multiple interacting species to landscape change.

In the half century since Preston (1962) first made the explicit analogy between habitat fragments and islands, there has been an explosion in the amount and variety of research being conducted under the umbrella of 'habitat fragmentation' (Ewers and Didham 2006, Collinge 2009). The sheer volume and intensity of focus on population-, species- and community-level responses to habitat change has drawn out increasingly divergent threads of theoretical and applied interest among fragmentation researchers. Separate reviews now synthesize findings specific to sub-disciplines, rather than the discipline as a whole (Ries et al. 2004, Kupfer et al. 2006, Ewers and Didham 2007a, Laurance and Curran 2008, Prugh et al. 2008). Although some of these branches of research, such as those focusing on nature reserve selection or corridors, might retain a tacit link to the early roots of the discipline in island biogeography theory (IBT) (MacArthur and Wilson 1967), some others, such as the study of edge effects or matrix contrast, focus as much on habitat quality as on spatial patterning. At face value, then, it might be fair to say that many branches of 'fragmentation' research are only comparatively loosely related within an expanding discipline. The question now is whether explicit recognition of habitat fragmentation as an over-arching conceptual domain will stimulate (Ewers and Didham 2007b) or hinder (Lindenmayer and Fischer 2007, Smith et al. 2009) further progress toward understanding and mitigating the effects of landscape change on biodiversity?

The conceptualization of diverse aspects of altered habitat quality as well as habitat quantity under the single banner of habitat fragmentation has been criticized by some as 'misleading in a concrete way [because] it directs attention to a contrast space that does not allow one to ask the specific questions…that need to be asked' (Haila 2002, p. 330), and by others as hampering efforts to understand and mitigate the impacts of landscape change, fuelling 'largely unproductive debates' (Lindenmayer and Fischer 2007, p. 127). However, we have argued that there is real heuristic value in explicit recognition of an over-arching domain that incorporates multiple interacting patterns and processes (Ewers and Didham 2007b, Didham 2010). Nevertheless, we do sympathize, to some extent, with the more general criticism that has punctuated the literature at increasingly frequent intervals that the conceptual underpinnings of habitat fragmentation research have lagged far behind empirical understanding of species responses to landscape change (Crome 1994, 1997, Harrison and Bruna 1999, Haila 2002, Fischer and Lindenmayer 2006, Lindenmayer and Fischer 2007). Our goal in this article is to encourage further development of the wider conceptual framework to the study of habitat fragmentation, so that it better reflects the spatial complexities and context-dependence of landscape effects that are now prevalent in the empirical literature (Ewers and Didham 2006, Fischer and Lindenmayer 2007, Didham 2010).

Polar dichotomies of thought

In our opinion, the key determinant of whether 'habitat fragmentation' can remain a cohesive framework lies in the concept of 'interdependence': 1) interdependence in the multiple pathways by which landscape and patch processes affect species and 2) interdependence in the responses of multiple species to landscape change. If there is non-trivial interdependence among the various spatial components of habitat fragmentation, or non-trivial interdependence among species responses to habitat change, then this would effectively negate their treatment as orthogonal variables (Ewers and Didham 2007b).

In attempting to integrate differing viewpoints in the literature, we have adopted Haila's (2002) approach of depicting the inherent assumptions underlying a research discipline as a 'conceptual phase space' (Fig. 1). We have chosen to represent this as two qualitative axes of contrasting false dichotomies in the habitat fragmentation problem space. Although many other (additional or alternative) representations of fragmentation problem space may be relevant, we have depicted what we believe are the two most contentious issues in the field. We outline the two major issues in this section, and then expand on each in turn in the following sections.

First, there has been a long-run emphasis placed on recognizing the apparent distinction between habitat loss and habitat fragmentation per se. Fahrig (2003, p. 509) concluded that 'Habitat loss should be called habitat loss; it has important effects on biodiversity that are *independent* of any effects of habitat fragmentation per se. Habitat fragmentation should be reserved for changes in habitat configuration that result from the breaking apart of habitat, *independent* of habitat loss' (emphasis added). The specific contrast being made in this case is the relative importance of habitat amount versus spatial arrangement, but the general principle is one of the degree of independence among multiple potential causal factors affecting species. Do these multiple drivers really act, or even occur, independently, as Fahrig (2003) implies? We argue that they do not, but the concept has been so widely accepted that it has already become an entrenched paradigm in the discipline. Instead, this concept might best be seen as one extreme in the degree of independence of habitat effects, at the other end of which lies complete context-dependence of habitat effects on species (Fig. 1). We suggest that conceptual unification is most likely to be achieved through an 'integrated drivers' concept, rather than through adherence to either extreme independence or extreme interdependence of habitat effects on species (Fig. 1).

Second, there has been sustained criticism that the dominant habitat fragmentation model is based on IBT, and that a strict IBT model is a poor predictor of how species respond to habitat change in real landscapes where the land-uses surrounding habitat patches are not necessarily inhospitable to patch-dwelling organisms (Haila 2002, Fischer and Lindenmayer 2006, Laurance 2008). IBT assumes that all species respond to spatial patterns of habitat in the

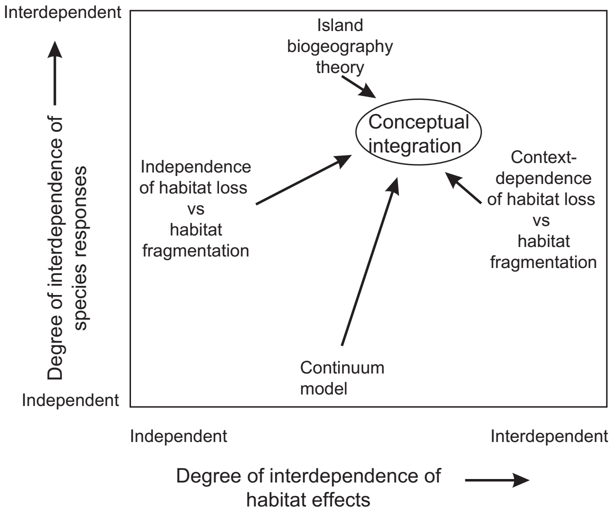


Figure 1. A conceptual phase space diagram (sensu Haila 2002) that characterizes the polarization of thought-patterns and ideas in habitat fragmentation research. The axes represent a qualitative scaling of background assumptions underlying different research approaches. First, the x-axis represents alternative views or assumptions about the degree of interdependence in the effects of multiple components of habitat loss and fragmentation on a specified response variable. At one extreme, it has been suggested that the effects of habitat fragmentation can only be determined after first taking into account the independent effect of habitat loss (Fahrig 2003), which implicitly assumes that the independent direct effects of multiple habitat drivers can be discriminated effectively. The alternative extreme is that multiple components of habitat loss and fragmentation are completely interdependent in their effects and operate through chains of indirect causal links. We suggest that neither of these alternatives is likely to be generalisable to all situations, but that interdependence of habitat effects will be the norm, rather than the exception. Second, the y-axis represents alternative views or assumptions about the degree of interdependence in the responses of multiple species to habitat loss and fragmentation. At one extreme (strict 'Island biogeography theory'), all species are assumed to respond in the same way to habitat fragmentation and there is no explicit consideration given to variation in individual species responses (Haila 2002). At the other extreme (the 'Continuum model'), species are assumed to have completely individualistic responses to habitat loss and fragmentation (Fischer and Lindenmayer 2006). We agree with Lortie et al. (2004) that neither of these alternatives is realistic under a wide range of circumstances, but that interdependence of species responses is likely to be the norm, rather than the exception.

same way, whereas Fischer and Lindenmayer (2006) make the valid point that no fragmentation model should implicitly assume that all species perceive the same human-defined patches as 'islands' of suitable habitat in an inhospitable matrix. However, there has been 40 years of research beyond the idealised IBT framework, which shows that individual species' responses to land-use change cannot be ignored, and we would argue that no fragmentation researchers now make such simplistic assumptions about the similarity of species responses. Nevertheless, IBT might well be seen as one extreme in the degree of interdependence (or covariance) of species responses to landscape change. At the other extreme, Fischer and Lindenmayer (2006) followed a suggestion made earlier by Haila (2002) and raised the 'continuum model', which makes the opposite assumption that species are distributed across ecological gradients according to their habitat needs in an entirely individualistic fashion. The specific contrast being made in this case is the relative utility of a discrete fragments-as-islands model versus a landscape-continuum model of species response, but the general principle is one of the degree of independence of species responses to landscape change. Do all species respond entirely independently to landscape change, as Fischer and Lindenmayer (2006) imply? We argue that they do not, and we reiterate the arguments put forward by Lortie et al. (2004) in their comprehensive rejection of the strict individualistic theory underlying the continuum model in plant community ecology. Instead, we suggest that the 'integrated community' concept of Lortie et al. (2004) will be found to be of great utility in the study of habitat fragmentation, as we outline in detail below (Fig. 1).

Independence or interdependence of habitat effects?

Are multiple components of landscape modification (e.g. habitat loss, patch isolation, edge effects and other components of spatial habitat configuration) collinear in their effects on species? One widely used definition of habitat fragmentation is the process by which habitat loss leads to a greater number of smaller patches of lower total area, isolated from each other by a matrix of dissimilar habitats (modified from Wilcove et al. 1986, Fahrig 2003). A key component of this definition is the inherent dependence of the resulting habitat configuration on the spatial and temporal progression of habitat loss (i.e. it is possible for habitat loss to occur without fragmentation, but it is not possible for fragmentation to occur without habitat loss). This dependence is borne out quite clearly in the strong intercorrelation among quantitative fragmentation metrics and the degree of habitat loss in the landscape (e.g. Fig. 3 in Fahrig 2003), and in universal scaling laws that have been reported for landscape fragmentation patterns (Fialkowski and Bitner 2008). The typical correlation structure for these types of data shows a broad overlap in the variance potentially attributable to habitat loss and the variance potentially attributable to habitat fragmentation per se (Fig. 2a). The intercorrelation problem became widely apparent with the development of a fully-fledged landscape perspective on habitat fragmentation in the 1990s. Earlier studies either ignored the intercorrelation of habitat fragmentation with habitat loss at the landscape scale, or made inappropriate landscape-level inference from patch-scale data. In doing so, these studies implicitly attributed all intercorrelated variance to habitat fragmentation (Fig. 2b). In order to redress the obvious flaws in this approach, several key studies highlighted the importance of discriminating habitat loss from habitat fragmentation per se (Andrén 1994, Fahrig 1997), and this has since become one of the defining paradigm shifts in the study of habitat fragmentation (Fahrig 2003, Collinge 2009). It has become de rigeur to first extract or control for the variance attributable to habitat loss before interpreting the remaining variance attributable to habitat fragmentation. Ironically, however, far from providing an 'independent' discrimination of habitat loss and habitat fragmentation per se, this approach (Fig. 2c) is no more valid in overcoming the intercorrelation problem than the earlier approach used in patch-biased studies, and differs only in the direction of the bias (Koper et al. 2007, Smith et al. 2009). The generalised conclusion from the landscape-biased perspective, that fragmentation has little or no effect on species richness after controlling for habitat loss, also stands at odds with the wealth of evidence for the ecological impact of variables such as patch area, edge effects and matrix contrast on communities (Didham 2010). What is needed instead is a means of partitioning the indirect contributions of habitat loss and fragmentation to the intercorrelated portion of variance (Fig. 2d).

We believe that one way to achieve integration of these divergent perspectives is to shift from a conceptual model that is based (either implicitly or explicitly) on the independent effects of landscape variables (a multiple regression model approach; Fig. 3a), to a conceptual model based on a hierarchical causal structure of direct and indirect effects among variables (a structural equation model approach; Fig. 3b). Although the raw intercorrelation between habitat loss and habitat fragmentation (Fig. 2) gives no indication of an inherent underlying set of causal relationships among variables, we would argue that the direction of causality, and the temporal sequence of events, is clearly operating from habitat loss to the resulting change in spatial arrangement (Fig. 3b) and not the other way around. A hierarchical causal model (such as the classical depiction in Fig. 3b, or a more hierarchical patch-within-landscape depiction of effects in Appendix 1, Fig. A1) would allow researchers to raise a formal distinction between the ultimate versus proximate effects of spatial variables, and provide a working platform for testing hypotheses about the degree of 'independence' of individual variables (Fig. 1). This, in turn, would allow the focus of the field to be redirected toward a new generation of more interesting fragmentation questions revolving around partitioning of the ultimate versus proximate and direct versus indirect effects of multiple drivers of landscape change. For example, a hierarchical causal model would help resolve the striking paradox between the landscape-biased conclusions that habitat fragmentation has negligible effects on biodiversity after habitat amount is taken into account, versus the conclusions of many thousands of patch-biased studies showing strong ecological effects of patch area, matrix hostility, edge effects and so on. The most parsimonious explanation for this apparent paradox is that the effects of habitat loss are mediated in large part by changing spatial

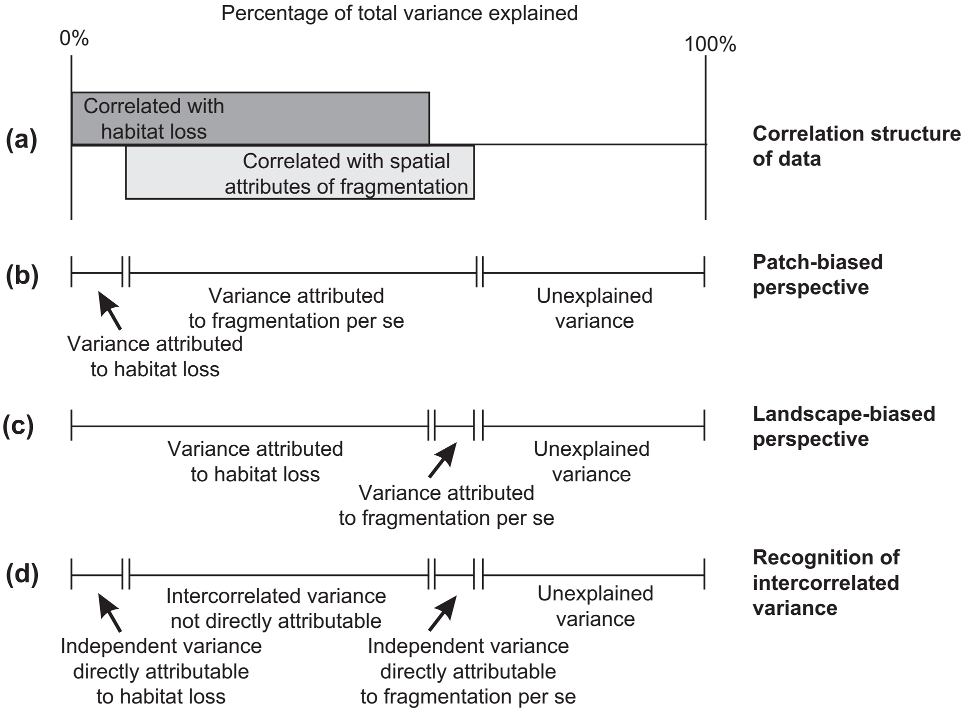


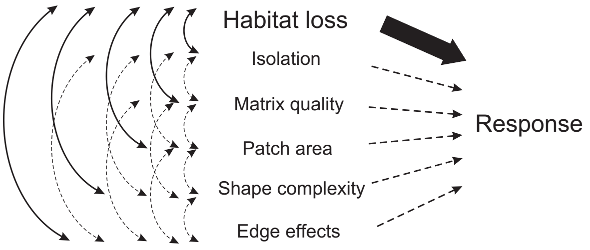
Figure 2. (a) A schematic representation of the problem of attributing causality to 'habitat loss' versus 'habitat fragmentation per se' (Fahrig 2003), when all measures of spatial habitat configuration are intrinsically dependent on the amount of remaining habitat. (b) Most studies have ignored the interdependence of habitat fragmentation with habitat loss at the landscape scale, or have made inappropriate landscape-level inference from patch-scale data, and have therefore implicitly attributed all intercorrelated variance to habitat fragmentation. (c) Widespread criticism of this approach led to the assertion that fragmentation measurements can only be made correctly at the landscape scale, after first taking into account the (supposedly) 'independent' effects of habitat loss (Fahrig 2003), and subsequent studies have therefore implicitly attributed all intercorrelated variance to habitat loss. (d) Neither of these approaches is valid because the intercorrelated variance is not directly attributable to either factor (d). However, causal inference can be made by interrogating the indirect relationships among spatial components of landscape change (Fig. 3).

arrangement of habitat – that is, habitat loss acts via the change in habitat arrangement, not *independently* of it.

Of course, across landscapes with differing land-use histories, and across species with differing traits, there will be strong empirical variation in the relative importance of direct versus indirect causal relationships between landscape and patch variables. In all cases, however, comparison of the standardized partial regression coefficients from a hierarchical causal model would allow a falsifiable test of whether habitat amount in the landscape is predominantly acting directly ('independently') on the response variable or whether it is (also) acting indirectly ('interdependently') via changing spatial arrangement of habitat (Fig. 1, 3b). In fragmented landscapes, such effects are likely to grade from independent to interdependent under differing circumstances, and we are certainly not suggesting that landscape variables will always operate interdependently (nor has such a suggestion been made in the literature, to our knowledge). Superficially, the pursuit of a falsifiable test for the relative influence of habitat amount and habitat configuration might sound like a very similar goal to that put forward by Fahrig and colleagues (Smith et al. 2009), but there is an important conceptual distinction between approaches. The partial regression coefficients calculated in a structural equation modeling approach are conceptually quite different to the partial regression coefficients derived from a multiple regression modeling approach, which (Smith et al. 2009, p. 1283) promote as 'unbiased estimates of the relative importance of [habitat] amount and fragmentation'. All the statistical methods compared by Smith et al. (2009) are based on the underlying assumption of independent effects of habitat amount and fragmentation in regression models, and ignore the interdependence of effects.

There are at least three important considerations in developing a hierarchical causal model for habitat fragmentation effects. First, the hierarchical nature of the causal relationships (i.e. edges within patches, patches within landscapes, and landscapes within regions) will inevitably demand different sampling strategies to adequately parameterise models, and different statistical techniques to analyse them (perhaps more akin to multi-level modelling, or hierarchical structural equation models; Shipley 2009), than those that are currently employed in most landscape-scale fragmentation studies (Smith et al. 2009). It will also radically alter the concept of independence of replicates, and force more critical consideration of the appropriate 'level' (of the model) at which to expend effort on increasing the number of replicates (e.g. replication at the patch level or replication at the landscape level). Fahrig's (1997, 2003) insight that landscape-level replication is critical to the discrimination of habitat loss versus habitat fragmentation per se holds true for a hierarchical causal modelling approach as well, but

(a) Correlative regression model



(b) Hierarchical causal model

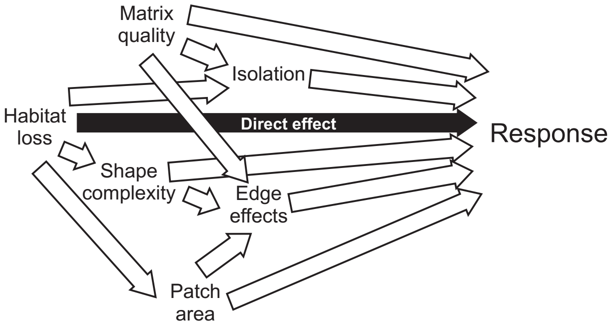


Figure 3. Competing models that treat habitat loss versus habitat fragmentation as either (a) independent or (b) interdependent effects. (a) A hypothetical multiple regression model of the putative direct drivers of biotic response to habitat loss and fragmentation (corresponding to the correlative data structure in Fig. 1c), showing how a 'landscape-biased approach' would force priority in the model to habitat loss (solid arrows) and subsume all of the variance intercorrelated with fragmentation (dotted arrows). (b) A hypothetical structural equation model showing how the effect of habitat loss not only operates directly and separately from the effects of habitat fragmentation, it also operates indirectly through pathways mediated by altered spatial configuration. For clarity, not all possible indirect pathways are shown in (b). See Appendix 1, Fig. A1 for a more detailed hierarchical representation. Models are expressed in path analytical notation with inferred causal paths indicated by single-headed arrows and correlations indicated by double-headed arrows.

not without replication within each landscape at the same time (cf. McGarigal and Cushman 2002). Determining the appropriate tradeoff between sampling effort and statistical power will be substantially more challenging under a hierarchical causal model.

Second, simple causal models (such as the one shown in Fig. 3b) that only incorporate the main (mediating) effects of spatial variables will never capture the full complexity of fragmentation effects. It is increasingly widely recognised that non-additive interaction effects occur among multiple spatial components of habitat arrangement (Ewers and Didham 2006, Ewers et al. 2007) and incorporation of these types of interaction effects into fragmentation models will be essential to adequately partition the direct and indirect drivers of system dynamics (Blakely and Didham 2010). The mechanistic pathways via which these interaction effects operate will need more careful consideration than is currently afforded in the fragmentation literature, with clear discrimination of whether one variable mediates the effects of another variable (giving rise to simple numerical 'interaction chain effects', Didham et al. 2007, which can be identified in a simple model like Fig. 3b) or moderates the effects of another variable (giving rise to functional shifts in per capita 'interaction modification effects', Didham et al. 2007).

Third, it is important to recognise that none of the spatial variables identified in causal models should be strictly considered 'effect mechanisms' in their own right. Instead, spatial variables operate through one or more proximate biotic or abiotic mechanisms that actually elicit population-, species-, community- or ecosystem-level responses (e.g. Fig. 4). For example, in the context of population demographic response to habitat fragmentation, it might be that birth rates are positively correlated with a measured spatial variable, such as habitat patch area, but the actual proximate factor that individuals are responding to might be some factor such as greater resource availability in larger patches (Fig. 4). Other population demographic parameters (births, immigration, deaths, or emigration) may even be affected in contrasting ways by the same or different spatial components of fragmentation acting via differing proximate effect mechanisms (Fig. 4; see also Fig. 1 in Hobbs and Yates 2003). As Didham (2010) points out, simply saying that habitat loss drives species response in this sort of hierarchical model is like saying that human population pressure drives habitat destruction; it is certainly true that it is the ultimate driver of change, but this provides no mechanistic understanding of the proximate ecological processes at work or how they might be addressed by management.

It seems evident that any conceptual framework based on either extreme independence or extreme interdependence of habitat effects on species will form a weak foundation for the study of habitat fragmentation. We suggest that conceptual unification is most likely to be achieved through an 'integrated drivers' concept, in which interdependence of

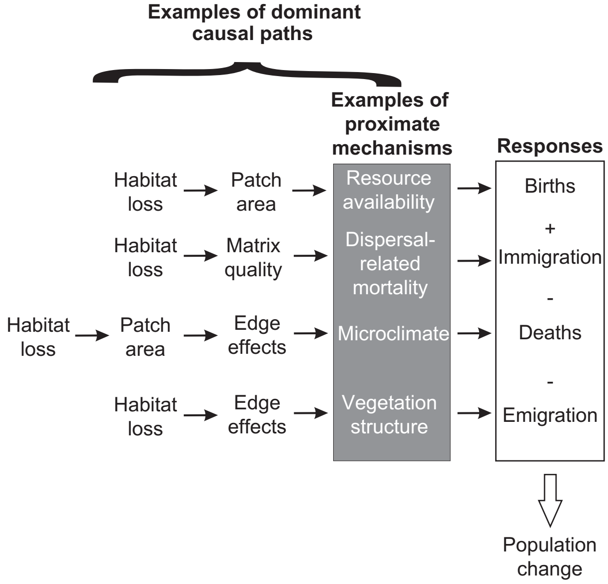


Figure 4. The spatial patterning of habitat does not, in itself, explain the mechanistic basis to the effects of habitat fragmentation on population change. The direct and indirect effects of altered habitat amount and spatial arrangement operate through a range of proximate mechanisms. Hypothetical examples are illustrated for possible causal paths leading to changes in births, immigration, deaths and emigration.

habitat effects will likely be the norm rather than the exception (Fig. 1). However, there should be clear recognition that quantitative partitioning of the direct versus indirect effects of spatial variables must be judged empirically on a case-by-case basis. This shift in emphasis in conceptual models toward the interdependence of habitat effects is not intended to downplay the significance of the earlier debate about the relative importance of the 'independent' effects of habitat loss versus habitat fragmentation per se (Fahrig 2003). This was clearly an important, perhaps necessary, step in the development of the field, but in many ways we see the escalating pursuit of 'independence' among multiple factors (Mortelliti et al. 2010) as a blind alley for mechanistic understanding of the ecological consequences of habitat fragmentation. Instead, greater mechanistic understanding lies in determining the structure of hierarchical causal models that incorporate the interdependent effects of multiple spatial variables.

Independence or interdependence of species responses?

Do multiple species covary in their responses to habitat fragmentation? This disarmingly simple question belies contentious debate over the most appropriate underlying conceptual model to characterise variation in species responses to fragmentation. Historically, much of this contention can be traced to a series of simplifying assumptions that were made in the earliest models adopting the fragments-as-islands analogy (Preston 1962), and applying IBT to the study of species responses in terrestrial habitat patches (Simberloff and Abele 1976). In its strict form, IBT considers just patch area and isolation, incorporates no external landscape dynamics beyond the probabilistic arrival of colonists across an inhospitable matrix, no internal patch dynamics beyond probabilistic extinction rates, and is 'neutral' to species identities or functional traits (Didham 2010). By extension, then, the IBT model assumes that all species perceive the matrix as hostile and respond to landscape structure in the same binary fashion (i.e. complete 'interdependence', or covariance, in species responses; Fig. 1).

Although the idealised IBT model was always well recognised as a caricature of how real species responded in real landscapes (Simberloff and Abele 1976), the dominant 'fragmentation model' in the literature has repeatedly been conflated with an 'IBT model' (Haila 2002, Fischer and Lindenmayer 2006). Consequently, much has been written about the lack of relevance of 'habitat fragmentation theory' to landscape ecology because the underlying basis in IBT does not fit the complexity of anthropogenically-modified landscapes, where strong external influences on patches are paramount and there is a blurring of the boundaries between what constitutes the 'patch' and the 'matrix' from the niche perspective of an organism (Haila 2002, Fischer and Lindenmayer 2006, Laurance 2008). Why this continual reversion to the idealised IBT origins of the field still persists in the literature is uncertain, given how far fragmentation research has advanced beyond IBT in the last 40 years (Laurance 2008). As Laurance (2008, p. 1739) puts it, the theory now seems 'simplistic to the point of being cartoonish'. Perhaps it is simply that the IBT model of fragmentation has always been the perfect foil against which to raise contrasting research findings (particularly with respect to varying species responses to patch quality, edge effects or matrix quality). Or perhaps the issue has been a lack of other formalised alternative models of species responses to fragmentation against which to compare or test empirical patterns, until recently. Initially, at least, this led to a wealth of descriptive anecdotes about idiosyncratic species responses to fragmentation (Ewers and Didham 2006), but comparatively little in the way of generalisations or theory of species response (but see Henle et al. 2004, Manning et al. 2004, Fischer and Lindenmayer 2006, Öckinger et al. 2010).

More recently, there has been a watershed in the development of alternative models of species response to landscape change, which has variously been viewed as evidence of rapid advances in the field or as evidence of an on-going 'identity crisis' in landscape ecology (Kent 2009). In many instances the proliferation of models has been described fairly prosaically in terms of an incremental methodological transition from categorical patch-based approaches to continuous gradient approaches to the study of landscape dynamics (McGarigal and Cushman 2005, Kent 2009, McGarigal et al. 2009). However, the deeper conceptual transition we see is from models that historically ignored any explicit variation in species responses to landscape change, such as the 'fragments-as-islands' patch model (Diamond and May 1976), the patch-corridor-matrix mosaic model (Forman 1995), and the landscape variegation model (McIntyre and Hobbs 1999), through to recent models that explicitly incorporate differences in species responses, such as the hierarchical patch model (Wu and David 2002, Dunn and Majer 2007) and variants of the continua-umwelt, contour and continuum models (Fischer et al. 2004, Manning et al. 2004, Fischer and Lindenmayer 2006, Lindenmayer et al. 2007). The latter models have gravitated (at least in an idealised form) toward a strict individualistic concept of species response to landscape change that was drawn from continuum theory in plant community ecology (Austin 1999), as described by Manning et al. (2004) and Fischer and Lindenmayer (2006). In these models, species are considered to be distributed along spatial and environmental gradients according to their specific habitat needs in an individualistic fashion (i.e. complete 'independence' of species responses; Fig. 1).

No more polarised dichotomy in species response models could be conceived (Fig. 1) and it is tempting to view the adoption of an individualistic species response model as a direct result of the death of the idealised IBT model and the conceptual vacuum of alternative response models in the intervening decades. On the other hand, the assumption of complete independence of species responses might simply reflect a natural modelling tendency toward an extreme idealised scenario of varying species responses. In either case, while proponents of individualistic response models have been promoting the adoption of vegetation continuum theory in landscape ecology (Fischer and Lindenmayer 2006), plant ecologists have moved in the opposite direction and rejected strict individualistic theory as a viable foundation for a general theory of community assembly (Lortie et al. 2004). Lortie et al. (2004) provide a compelling synthesis of the quiet revolution that has taken place in understanding the over-riding importance of facilitation, indirect interactions and interaction modification effects to plant community assembly. The prevalence of these interactions in nature suggests a much greater interdependence in plant species occurrence (and response to landscape structure) than the traditional individualistic perspective can explain. Moreover, Lortie et al. (2004, p. 434) suggest that 'interdependence may be the norm within communities particularly (but not exclusively) when multiple trophic levels are considered', as in the application of continuum theory to fauna research (cf. Fischer and Lindenmayer 2006). Given these considerations, Lortie et al. (2004) call on (plant) ecologists to reject strict individualistic theory and embrace interdependence of species responses as a way to better explain variation in species distributions and predict community-level responses to global change.

As an alternative to individualistic theory, Lortie et al. (2004) introduced the 'integrated community concept' which proposes that natural communities range from highly individualistic to highly interdependent depending on 'synergistic (non-[additive]) interactions among 1) stochastic processes, 2) the specific tolerances of species to the suite of local abiotic conditions, 3) positive and negative direct and indirect interactions [within trophic levels], and 4) [positive and negative] direct [and indirect] interactions [between trophic levels]' (adapted from the plant community perspective of Lortie et al. 2004, p. 434). This is analogous to the qualitative variation in degree of independence of species responses proposed on the vertical axis of Fig. 1, and we suggest that the integrated community concept will find great utility in the study of species responses to habitat fragmentation. In Appendix 1, Fig. A2, we extend our earlier hierarchical causal model of interdependent habitat effects (Fig. 3b, 4) to incorporate interdependence in species responses, producing a stylization of community assembly or disassembly under interdependence of both habitat effects and species responses. There will certainly be many alternative ways of incorporating interdependence among species into new or existing models. It is also worth considering whether the framing of the integrated community concept in a spatially-explicit landscape context (i.e. a 'spatially-integrated community concept') might effectively be just another way of voicing a 'metacommunity concept' of community assembly (Gonzalez 2009).

Despite the conceptual gulf that exists between Fischer and Lindenmayer (2006) and Lortie et al. (2004) in their theoretical treatment of independent versus interdependent species responses (respectively), there are some surprising similarities in the mechanics of their models, which both include species interaction processes such as competition and predation (and therefore imply interdependence among species responses). It is also clear from recent debate in the literature (Fischer and Lindenmayer 2006, Dunn and Majer 2007, Lindenmayer et al. 2007), that proponents of the landscape continuum model support pluralism in landscape models (Lindenmayer et al. 2007, Kent 2009, Price et al. 2009). While 'pluralism' in approaches might be one implicit way to allow for interdependence under some circumstances, we do not see why interdependence could not be explicitly factored into a single generalised model of species responses to landscape dynamics.

We argue that strict individualistic species response models will hinder predictive understanding in the study of habitat fragmentation. The full connotation of a formal individualistic concept is accurately captured by Manning et al. (2004, p. 627), when they state that "the daunting implication of [an assumption of individualistic species responses] is that there are as many landscapes as there are organisms". Is it really useful to think of all species as having different landscape dynamics? To paraphrase the famous words of Lawton (1992): just because there are ten million or so species of plants and animals on Earth, does that really mean there are ten million kinds of landscape dynamics? At one level the answer is yes, there is infinite variation in spatiotemporal dynamics across species and landscapes. At quite another level the answer is a resounding no, 'there are not ten million kinds of [landscape] dynamics; rather there are a multitude of essentially trivial variations on a few common themes' (Lawton 1992, p. 337). Within biogeography, there is a good deal of historical irony in these words. In 1974, Daniel Simberloff marvelled at how IBT, within a single decade, had transformed biogeography from a descriptive 'idiographic' art revelling in the complexity and uniqueness of historical patterns, to a predictive 'nomothetic' science searching for generalised patterns, underlying principles, and laws of nature (Simberloff 1974). In the past decade, the rise of individualistic species response models is seeing landscape ecology track the reverse path back toward phenomenological complexity and idiosyncracy. We do not see this as a positive outcome.

In response to the question posed at the start of this section: yes, we believe there is unequivocal evidence that at least some species (frequently many) do covary in their responses to habitat fragmentation; but no, not all species respond in the same way. Variation in the patterns and processes of species responses to fragmentation is essential to incorporate into landscape models, but any model based on a strict individualistic concept of species responses will be a poor reflection of reality. More broadly, it seems evident that any conceptual framework based on either extreme independence or extreme interdependence of species responses to landscape change will form a weak foundation for the study of habitat fragmentation. We agree with Lortie et al. (2004) that conceptual unification is most likely to be achieved through an 'integrated community' concept in which interdependence of species responses is likely to be the norm, rather than the exception (Fig. 1).

Conclusions

The conceptual foundations of habitat fragmentation research have not kept pace with empirical advances in our understanding of species responses to landscape change, or theoretical advances in the wider disciplines of ecology. The current paradigms that are becoming entrenched in the fragmentation literature are implicitly founded on strict independence of habitat effects on species and strict independence of individualistic species responses to landscape change, despite compelling evidence for interdependence in both effects and responses to fragmentation. Arguably, it might be sufficient to merely expose the underlying conceptual dichotomies that are evident in the literature, and let the degree of interdependence of habitat effects and degree of interdependence of species responses be judged empirically, on a case-by-case basis. However, we believe there are compelling theoretical reasons why we might expect, a priori, that 'independence' will be the exception, rather than the norm, in determining the ecological consequences of habitat fragmentation. In fact, we see the conceptual notion of 'independence' of effects and responses as a blind alley for mechanistic understanding of habitat fragmentation in its broadest sense (Ewers and Didham 2007b). Instead, 'interdependence' of effects and responses challenges us to rethink long-held views, and re-cast the conceptual foundations of habitat fragmentation in terms of spatial context-dependence in the effects of multiple interacting drivers of habitat fragmentation, and community context-dependence in the responses of multiple interacting species to landscape change.

Acknowledgements – The ideas put forward in this paper benefited from stimulating discussions with Lenore Fahrig, Gonçalo Ferraz, Andy Hector and Bob Holt at the 'Testable hypotheses in fragmentation research' workshop organised by RME at Imperial College London, UK, 16–20 February 2009. We thank Richard Hobbs, Tatyana Rand, Rachel Standish and Jason Tylianakis for thoughtful comments on earlier versions of the manuscript.

References

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – Oikos 71: 355–366.

Austin, M. P. 1999. A silent clash of paradigms: some inconsistencies in community ecology. – Oikos 86: 170–178.

Blakely, T. J. and Didham, R. K. 2010. Disentangling the mechanistic drivers of ecosystem-size effects on species diversity. – J. Anim. Ecol. 79: 1204–1214.

Collinge, S. K. 2009. Ecology of fragmented landscapes. – The Johns Hopkins Univ. Press.

Crome, F. H. J. 1994. Tropical forest fragmentation: some conceptual and methodological issues. – In: Moritz, C. and Kikkawa, J. (eds), Conservation biology in Australia and Oceania. Surrey Beatty and Sons, pp. 61–76.

Crome, F. H. J. 1997. Researching tropical forest fragmentation: shall we keep on doing what we're doing? – In: Laurance, W. F. and Bierregaard, R. O. (eds), Tropical forest remnants: ecology, management and conservation of fragmented communities. Univ. of Chicago Press, pp. 485–501.

Diamond, J. M. and May, R. M. 1976. Island biogeography and the design of nature reserves. – In: May, R. M. (ed.), Theoretical ecology. Principles and application. Blackwell, pp. 163–186.

Didham, R. K. 2010. Ecological consequences of habitat fragmentation. Encyclopedia of Life Sciences. – Wiley.

Didham, R. K. et al. 2007. Interactive effects of habitat modification and species invasion on native species decline. – Trends Ecol. Evol. 22: 489–496.

Dunn, A. G. and Majer, J. D. 2007. In response to the continuum model for fauna research: a hierarchical, patch-based model of landscape patterns. – Oikos 116: 1413–1418.

Ewers, R. M. and Didham, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. – Biol. Rev. 81: 117–142.

Ewers, R. M. and Didham, R. K. 2007a. The effect of fragment shape and species' sensitivity to habitat edges on animal population size. – Conserv. Biol. 21: 926–936.

Ewers, R. M. and Didham, R. K. 2007b. Habitat fragmentation: panchreston or paradigm? – Trends Ecol. Evol. 22: 511.

Ewers, R. M. et al. 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. – Ecology 88: 96–106.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. – J. Wildlife Manage. 61: 603–610.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – Annu. Rev. Ecol. Syst. 34: 487–515.

Fialkowski, M. and Bitner, A. 2008. Universal rules for fragmentation of land by humans. – Landscape Ecol. 23: 1013–1022.

Fischer, J. and Lindenmayer, D. B. 2006. Beyond fragmentation: the continuum model for fauna research and conservation human-modified landscapes. – Oikos 112: 473–480.

Fischer, J. and Lindenmayer, D. B. 2007. Landscape modification and habitat fragmentation: a synthesis. – Global Ecol. Biogeogr. 16: 265–280.

Fischer, J. et al. 2004. Appreciating ecological complexity: habitat contours as a conceptual model. – Conserv. Biol. 18: 1245–1253.

Forman, R. T. T. 1995. Land mosaics: the ecology of landscapes and regions. – Cambridge Univ. Press.

Gonzalez, A. 2009. Metacommunities: spatial community ecology. Encyclopedia of Life Sciences. – Wiley.

Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. – Ecol. Appl. 12: 321–334.

Harrison, S. and Bruna, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? – Ecography 22: 225–232.

Henle, K. et al. 2004. Predictors of species sensitivity to fragmentation. – Biodiv. Conserv. 13: 207–251.

Hobbs, R. J. and Yates, C. J. 2003. Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. – Aust. J. Bot. 51: 471–488.

Kent, M. 2009. Biogeography and landscape ecology: the way forward – gradients and graph theory. – Progr. Phys. Geogr. 33: 424–436.

Koper, N. et al. 2007. Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: implications for the debate. – Landscape Ecol. 22: 811–820.

Kupfer, J. A. et al. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. – Global Ecol. Biogeogr. 15: 8–20.

Laurance, W. F. 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. – Biol. Conserv. 141: 1731–1744.

Laurance, W. F. and Curran, T. J. 2008. Impacts of wind disturbance on fragmented tropical forests: a review and synthesis. – Austral Ecol. 33: 399–408.

Lawton, J. H. 1992. There are not 10 million kinds of population dynamics. – Oikos 63: 337–338.

Lindenmayer, D. B. and Fischer, J. 2007. Tackling the habitat fragmentation panchreston. – Trends Ecol. Evol. 22: 127–132.

Lindenmayer, D. B. et al. 2007. The need for pluralism in landscale models: a reply to Dunn and Majer. – Oikos 116: 1419–1421.

Lortie, C. J. et al. 2004. Rethinking plant community theory. – Oikos 107: 433–438.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.

Manning, A. D. et al. 2004. Continua and Umwelt: novel perspectives on viewing landscapes. – Oikos 104: 621–628.

McGarigal, K. and Cushman, S. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. – Ecol. Appl. 12: 335–345.

McGarigal, K. and Cushman, S. A. 2005. The gradient concept of landscape structure. – In: Wiens, J. A. and Moss, M. R. (eds), Issues and perspectives in landscape ecology. Cambridge Univ. Press, pp. 112–119.

McGarigal, K. et al. 2009. Surface metrics: an alternative to patch metrics for the quantification of landscape structure. – Landscape Ecol. 24: 433–450.

McIntyre, S. and Hobbs, R. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. – Conserv. Biol. 13: 1282–1292.

Mortelliti, A. et al. 2010. Independent effects of habitat loss, habitat fragmentation and structural connectivity on forest-dependent birds. – Divers. Distrib. 16: 941–951.

Öckinger, E. et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. – Ecol. Lett. 13: 969–979.

Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part II. – Ecology 43: 410–432.

Price, B. et al. 2009. Continuum or discrete patch landscape models for savanna birds? Towards a pluralistic approach. – Ecography 32: 745–756.

Prugh, L. R. et al. 2008. Effect of habitat area and isolation on fragmented animal populations. – Proc. Natl Acad. Sci. USA 105: 20770–20775.

Ries, L. et al. 2004. Ecological responses to habitat edges: mechanisms, models and variability explained. – Annu. Rev. Ecol. Evol. Syst. 35: 491–522.

Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. – Ecology 90: 363–368.

Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. – Annu. Rev. Ecol. Syst. 5: 161–82.

Simberloff, D. S. and Abele, L. G. 1976. Island biogeography theory and conservation practice. – Science 191: 285–286.

Smith, A. C. et al. 2009. Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. – Landscape Ecol. 24: 1271–1285.

Wilcove, D. S. et al. 1986. Habitat fragmentation in the temperate zone. – In: Soulé, M. E. (ed.), Conservation biology. The science of scarcity and diversity. Sinauer, pp. 237–256.

Wu, J. G. and David, J. L. 2002. A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. – Ecol. Modell. 153: 7–26.

Appendix 1

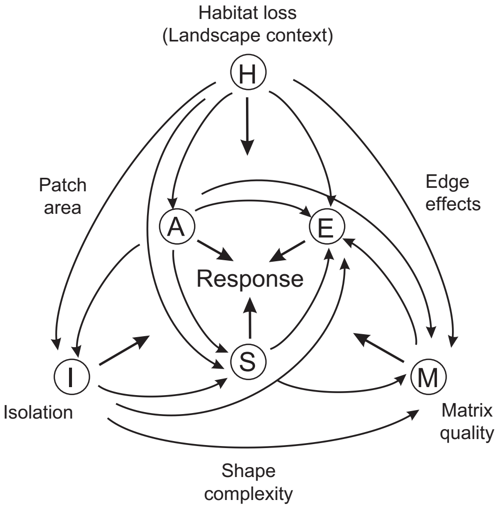


Figure A1. A hierarchical conceptual model of potential direct and indirect causal paths by which the amount and spatial arrangement of habitat can affect a measured response variable (termed ‘Response’). This model follows from the definition of ‘habitat fragmentation’ as a process by which habitat loss leads to a greater number of smaller patches of lower total area, isolated from each other by a matrix of dissimilar habitats (modified from Wilcove et al. 1986, Fahrig 2003). The outermost variables habitat loss (H), matrix quality (M) and isolation (I) are measures of habitat quantity and quality in the landscape surrounding a patch or patches, each of which has patch-level attributes of patch area (A), patch shape complexity (S) and patch edges (E). Arrow heads indicating the direction of causal inference are hypothetical and indicative only, because the direction of causality may vary for a given response variable, at a given place or time. For any given response variable, application of the model may only involve a subset of the full range of potential paths. Note that the model is only relevant as a test of the hypothesis that habitat loss and habitat fragmentation affect a given response variable, and may give misleading conclusions if potential interactions with other global change drivers (e.g. climate change, atmospheric CO_2 increase, nitrogen deposition, or species invasion) are not included in causal models. Note, also, that spatial measures of habitat quantity or quality are not, in themselves, mechanisms of effect. Each direct path will operate through a range of potential proximate mechanisms (Fig. 4).

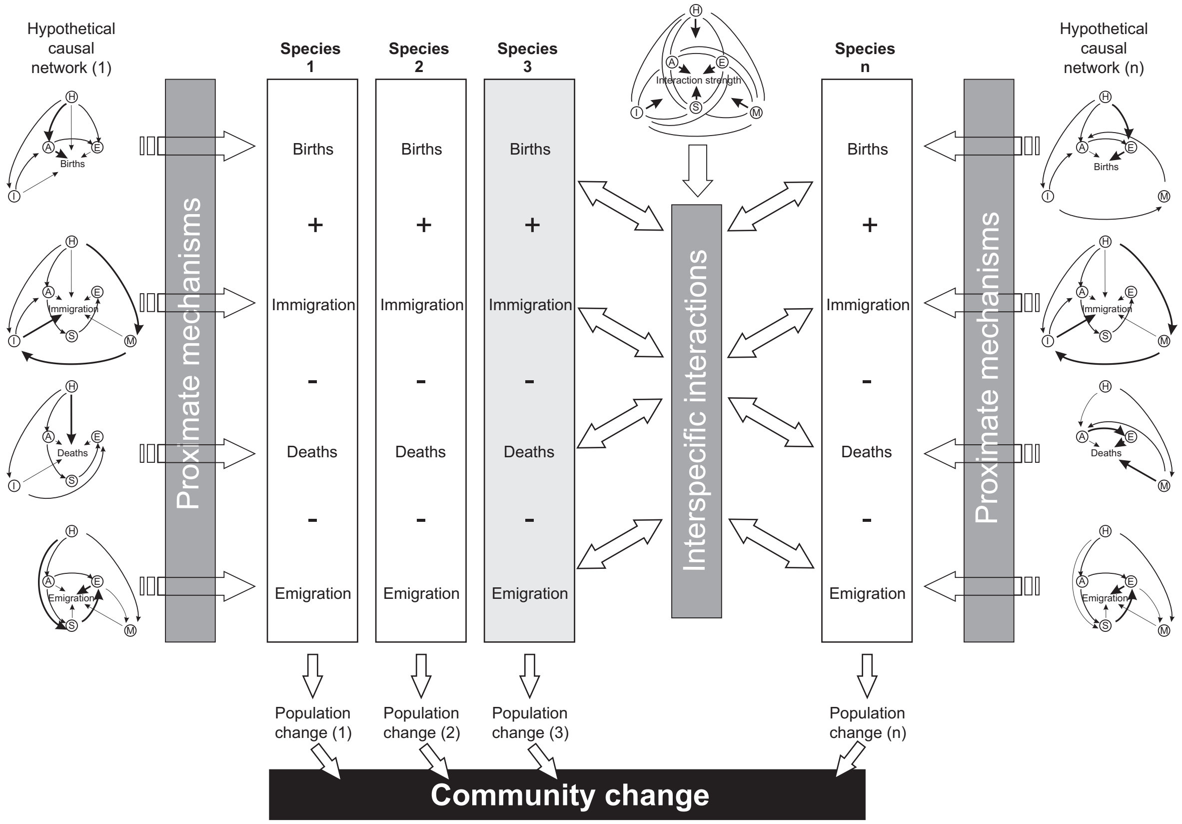


Figure A2. One of the central tenets of landscape ecology is that different species perceive, and respond to, different components of the spatial structure of landscapes in different ways. In fact, this is a gross over-simplification of the network of causal mechanisms that drive population-, species- and community-level changes in fragmented landscapes. The amount and spatial arrangement of habitat will have differing effects on different population demographic parameters (shown in a births-immigration-deaths-emigration, BIDE, framework) for different species (with hypothetical direct and indirect causal networks shown for species '1' and species 'n' in an n-species community). Note that direct drivers operate through a range of proximate mechanisms (Fig. 4). Implicit in the population dynamics framework is the notion of strong temporal, as well as spatial, variability in the relative strength and importance of different causal factors (for example, a change in immigration or emigration can affect the relative importance of factors affecting birth or death rates). Even if a particular species does not respond to habitat fragmentation directly, the spatial structure of the landscape may alter population abundance indirectly via a change in species interactions mediated by the increase or decrease in a consumer or resource due to landscape modification, or via a change in species interactions moderated by a per capita or per unit biomass change in the interaction strength of a consumer or resource due to landscape modification, without there necessarily being a change in the consumer or resource abundance (Didham et al. 2007). These direct and indirect effects of altered species abundances may involve invasive species (species 3, shaded).