



Review article

Confounding of patch quality and matrix effects in herbivore movement studies

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Abstract

Although the landscape matrix is increasingly incorporated into spatial-ecological population studies, little consideration has been given to the likely possibility that patch quality is confounded with the composition of the matrix surrounding each patch. For example, the nutritional quality of host-plant patches to an herbivore may be highly correlated with matrix composition, consequently obfuscating the importance of the matrix itself to inter-patch dispersal. From a literature survey of the effects of the matrix on herbivore movement among host-plant patches, we found that 55% of the studies (6/11) failed to experimentally or statistically isolate the effects of the matrix from potential patch-quality effects on dispersal. Most studies consisted of mark-recapture experiments in natural landscapes where patch equality was not controlled or manipulated. Of the few studies that evaluated the relationship between matrix composition and patch quality, all of them (3/3) found that these two landscape factors covaried. These data suggest that in most matrix studies, effects of the matrix on dispersal may be wholly, or in part, due to underlying differences in patch quality.

Introduction

Traditionally, metapopulation studies have emphasized the roles of patch size and isolation on the connectivity among patches (e.g., Thomas and Harrison 1992; Hanski 1994; Hill et al. 1996). In recent years, empirical and theoretical studies have considered the effects of the intervening habitat (i.e., the landscape matrix) on the movement of animals among patches (Taylor et al. 1993; Wiens 1997; Tischendorf and Fahrig 2000). For herbivores distributed among discrete host-plant patches, the general consensus is that the matrix matters (reviewed in Ricketts 2001; Cronin 2003). This conclusion may be premature because matrix studies have tended to ignore the confounding effects of other factors, most notably, host-plant patch quality.

Here, we describe how matrix composition frequently may covary with patch quality in plant-herbi-

vore systems. In addition, we review the literature on the effects of matrix composition on the interpatch movement of herbivores. Our purpose was to evaluate whether the hypothesis that matrix composition directly influences dispersal and landscape connectivity has been adequately tested. Although we have placed the focus of this paper on movement and connectivity, we recognize that matrix structure may also influence a variety of other processes such as habitat selection (Best et al. 2001; Lawler and Edwards 2002), response to patch edges (Cronin 2003; Haynes and Cronin 2003), and risk of predation (Wilcove 1985; Roos 2002). We chose to focus on connectivity because it represents a key parameter involved in determining the structure, dynamics and persistence time of subdivided populations (Hanski 1999). Finally, we suggest how future studies can provide more definitive tests of matrix effects on movement,

and discuss the value of integrating patch quality into dispersal studies conducted at the landscape scale.

Confounding of matrix effects and patch quality

The characteristics of vegetation patches (e.g., species composition, tissue-nitrogen levels, vegetation structure) may often vary with the composition of the surrounding matrix (Wiens et al. 1985; Pickett and Cadenasso 1995). Thus, the quality of host-plant patches to herbivores may often depend on the type of matrix within which the patches are embedded. For example, Haynes and Cronin (2003) found that leaf-nitrogen levels in patches of prairie cordgrass were significantly higher in mudflat- as compared to grass-embedded patches. The higher densities of specialized delphacid planthoppers in the former patches may be due to reduced emigration from patches bearing more nutritious host plants (see also Cook and Denno 1994). Similarly, laboratory feeding trials with the chrysomelid beetle *Acalymma innubum*, showed that this specialist herbivore preferentially fed upon leaves from patches of the cucurbit *Cayoponia americana* growing outside of a forest relative to leaves from patches growing at the forest edge (Bach 1984). Effects of forest canopy shading on leaf chemistry and toughness were suggested as explanations for the greater preference for leaves from patches growing in the open (Bach 1984).

Patch quality might vary with the type of surrounding matrix for the following three reasons. First, background abiotic conditions (e.g., edaphic characteristics, topography) may determine host-plant quality, as well as the distributions of both host-plant patches and matrix types (Wiens et al. 1985). Despite a lack of concrete examples in matrix studies, this would appear to be a likely scenario given that soil characteristics such as nutrient availability are known to influence both plant species distributions (Parker 1991; Swaine 1996; Sultan et al. 1998) and the nutritional quality of plants to specialist herbivores (Feller 1995; Moon et al. 2000; Gratton and Denno 2003). Second, the quality of the patch may be influenced by the type of bordering matrix. Matrix plants may interact with patch plants at the patch-matrix edge via competition for light, space, or nutrients and thus reduce the overall quality of patch plants. The strength of this effect will likely vary depending on the composition of the matrix. For example, by planting three types of matrix vegetation (tomatoes planted in the

ground, tomatoes in pots, no tomatoes) around small host plant patches (squash), Bach (1988) demonstrated that below-ground competition with matrix vegetation caused a reduction in the growth of the host plants. In addition, the matrix effect on patch quality need not be restricted to the patch perimeter. The matrix can influence large-scale flows of water, wind, and fire well into the interior of patches (Wiens et al. 1985; Pickett and Cadenasso 1995; Gascon et al. 2000; Weathers et al. 2001). For example, fires originating in agricultural matrix can penetrate deeply into Amazonian forest remnants, leading to the degradation and eventual demise of the forest (Gascon et al. 2000; Cochrane and Laurance 2002). Third, patch quality could potentially influence the composition of the surrounding matrix through the same mechanisms outlined above. Irrespective of the underlying causes, close associations between patch quality and the nearby landscape matrix may be common in many plant-herbivore systems, particularly those with distinctly different matrix types (e.g., a pasture versus forest matrix; Kuussaari et al. 1996).

For an herbivore, the quality of host plant patches can be a major factor influencing interpatch dispersal rates. Most of the existing information on this subject involves the study of spatially structured butterfly populations. Butterflies may respond to a low density of nectar producing flowers (an indicator of patch quality) either by increasing emigration (Gilbert and Singer 1973; Kuussaari et al. 1996) or decreasing immigration (Kuussaari et al. 1996; Matter and Roland 2002). In addition, Hanski et al. (2002) found that female *Melitaea cinxia* exhibit higher emigration from patches containing only the less preferred of two potential host plants used for oviposition. Consequently, if patch quality and the type of surrounding matrix frequently covary, previous reports of a matrix effect on dispersal (Table 1) may actually be flawed because the matrix effect is confounded with patch quality.

Literature review

Methodology

We searched the following journals from 1970 to the present for studies that examined the effects of matrix composition on some aspect of herbivore movement among suitable host-plant patches (e.g., emigration, immigration, patch transfer): *American Naturalist*, *Biological Control*, *Canadian Entomolo-*

Table 1. Study systems in which matrix effect on herbivore dispersal among host-plant patches was examined. We report whether a matrix effect was adequately demonstrated based on one of two criteria, whether the authors (1) experimentally controlled patch quality or randomly distributed patches of unknown quality among matrix treatments, or (2) directly quantified movement within each matrix type in the absence of suitable patches. An affirmative response to either criteria fulfilled our requirement for demonstrating a direct matrix effect. We also report whether the authors tested for patch quality effects on interpatch movement, and whether patch quality varied with matrix type. Finally, we list whether the study was performed in a landscape consisting of natural or experimentally created patches.

Species	Matrix effect adequately demonstrated?	Criteria		Tests performed		Patches natural or experimental?	References
		Quality constant or randomly distributed?	Within-matrix movement?	Quality effects on movement?	Matrix-quality association?		
<i>Battus philenor</i>	Yes	Yes	No	No	No	Natural	Rausher 1981
<i>Acalymma innubum</i>	No	No	No	No	No	Natural	Bach 1984
<i>Phyllotreta</i> beetles	Yes	Yes	No	No	No	Experimental	Kareiva 1985
Chrysomelid beetles	Yes	Yes	No	Yes	Yes	Experimental	Bach 1988 Lawrence and Bach 1989
<i>Melitaea cinxia</i>	No	No	No	Yes	No	Natural	Kuussaari et al. 1996
<i>Metrioptera bicolor</i>	No	No	No	No	No	Natural	Kindvall 1999
<i>Aphthona</i> beetles	No	No	No	No	No	Natural	Jonsen et al. 2001
butterflies	No	No	No	Yes	No	Natural	Ries and Debinski 2001
butterflies	No	No	No	Yes	No	Natural	Ricketts 2001
<i>Trirhabda borealis</i>	Yes	Yes	Yes	No	No	Experimental	Goodwin and Fahrig 2002a Goodwin and Fahrig 2002b
<i>Prokelisia crocea</i>	Yes	Yes	No	No	Yes	Experimental	Haynes and Cronin 2003

gist, *Ecology*, *Ecological Entomology*, *Environmental Entomology*, *Journal of Animal Ecology*, *Journal of Applied Entomology*, *Journal of Economic Entomology*, *Journal of Insect Behaviour*, *Landscape Ecology*, *Oecologia*, and *Oikos*. We only included papers whose studies described clearly defined patches and more than one matrix type. Corridor studies were therefore excluded from the search (e.g., Fahrig and Merriam 1985; Aars and Ims 1999). Similarly, we excluded studies in which species readily utilize at least one type of matrix habitat as a source of nutrition (e.g., Pither and Taylor 1998; Roland et al. 2000). The search was conducted using Web of Science (<http://isi1.isiknowledge.com>) with the following keywords: *connectivity*, *dispersal*, *emigration*, *fragmentation*, *immigration*, *landscape*, *matrix*, and *movement*. In addition, we included our own in-press study (Haynes and Cronin 2003). For each study meeting our criteria, we evaluated whether the matrix effect could be distinguished from a patch-quality effect on herbivore movement. An effect of matrix composition on interpatch dispersal cannot be proven without experimentally manipulating the matrix and having patch quality be made constant (by growing plants in a common garden) or randomly distributed among matrix treatments, *or* by directly quantifying movement (e.g., net displacement, path tortuosity) within different matrix types in the absence of nearby patches. The incorporation of one or more patch-quality measures (among the many that are possible) into the analysis of a matrix effect, e.g., as covariates, was not considered sufficient to rule out patch quality as a confounding factor. To further elucidate the possible relationship between patch quality and the matrix, we asked three subsidiary questions from each study system: 1) was there an assessment of whether patch quality varied with the composition of the matrix; 2) was there a test to determine whether patch quality influenced movement; and 3) were the patches in the study landscape natural or experimentally created? In addressing these questions, we drew from all published work associated with each particular study system, and combined publications on the same study system as a single study (chrysomelid beetles: Bach 1988, Lawrence and Bach 1989; *Trirhabda borealis*: Goodwin and Fahrig 2002a; Goodwin and Fahrig 2002b).

Results and conclusions

We found eleven studies suitable for inclusion in this review, all of which focused on phytophagous insects. Admittedly, our search did not yield a large number of studies, no doubt a result of the recent popularity of the subject of matrix effects on dispersal and landscape-level dynamics and the difficulty in performing these studies. However, we felt it important to call attention to the issue of reporting significant matrix effects on herbivore movement when the effects may in fact be due to variation in patch quality. More than one-half of the studies (6/11) did not meet our criteria for establishing that matrix composition influenced interpatch movement rates, independent of patch quality (Table 1). All of the studies that did not establish a direct matrix effect on movement were conducted in naturally occurring patches (i.e., those not created experimentally). Under these circumstances, patch quality and the type of surrounding matrix may covary (Wiens et al. 1985; Pickett and Cadenasso 1995). In fact, for all three studies that examined the covariation between the matrix and patch quality (*Acalymma innubum*: Bach 1984; chrysomelid beetles: Bach 1988; Lawrence and Bach 1989; *Prokelisia crocea*: Haynes and Cronin 2003), a significant relationship was detected. Given the strong effects of patch quality on emigration and immigration in many systems (e.g., Kuussarri et al. 1996; Matter and Roland 2002), differences in interpatch movement rates that were attributed to matrix types actually may have been due, in whole or in part, to patch quality differences among matrix types (Haynes and Cronin 2003). The jury on whether the matrix matters (*sensu* Ricketts 2001) is still out in six of eleven cases.

Of the five studies that provided convincing evidence that the observed matrix effects on interpatch dispersal were not due to the confounding effects of patch quality, three were performed in experimental landscapes in which patches were formed from potted plants grown under common garden conditions (Kareiva 1985; Bach 1988; Haynes and Cronin 2003). In the remaining two studies (Rausher 1981; Goodwin and Fahrig 2002a), the matrix treatments were randomly distributed among patches. Thus, systematic bias in patch quality among matrix types was unlikely. In one of the latter studies, matrix effects on movement were also determined directly by tracking individuals through different matrix types (Goodwin and Fahrig 2002b).

It was not our intention with this paper to make a blanket criticism of large-scale, non-manipulative studies. For several studies in naturally occurring patches, the species were either endangered (the Glanville fritillary, Kuussaari et al. 1996), the ecosystem imperiled (tall-grass prairie, Ries and Debinski 2001), or the scale of movement too large (Kuussaari et al. 1996; Ries and Debinski 2001; Ricketts 2001), rendering landscape manipulations impractical. For such species, studies conducted in small experimental patch networks would be biologically meaningless.

Recommendations

We feel that there are certain steps that can be taken to more clearly differentiate the roles of matrix structure and patch quality on interpatch movement when landscape manipulations are not possible. First, measurements of movement rates among natural patches embedded in different matrix types can be coupled with dispersal experiments that directly examine movement patterns *within* each matrix type (e.g., Goodwin and Fahrig 2001b; Haynes and Cronin unpublished data). Second, we recommend that ecologists examine whether patch quality varies with matrix composition (Table 1). Finally, ecologists should examine patch-quality effects on dispersal, ideally through the direct manipulation of patch quality attributes. For many large-scale systems, this may be surprisingly easy. A good example is the work by Matter and Roland (2002) in which the removal of nectar-producing flowers from meadows reduced immigration rates of male alpine butterflies (*Parnassius smintheus*). Four of the studies listed in Table 1 did test patch quality effects on movement, however, these tests were generally correlative (Kuussaari et al. 1996; Ricketts 2001; Ries and Debinski 2001). The pitfall to this approach is that patch-quality variables not considered may also influence movement.

To definitively ascertain a matrix effect on dispersal and population dynamics, variation in patch quality must be experimentally controlled or manipulated. Ideally, dispersal studies are needed in which patch quality, patch size, and matrix composition are manipulated independently; e.g., by using experimentally created patches. Besides elucidating the direct effects of landscape attributes on dispersal, a controlled experiment can reveal potential interactive effects of different landscape variables. Patch quality

and matrix composition may affect dispersal synergistically or antagonistically rather than additively. For example, emigration rates from host-plant patches may be greatly reduced when patches of high nutritional quality are coupled with a resistant matrix (i.e., one inhibiting emigration). In contrast, other matrix types may favor such high emigration rates that patch-quality effects are overridden. To date, both empirical studies and metapopulation/landscape models have ignored possible interactive effects of landscape variables on dispersal and population dynamics. We conclude that a more comprehensive approach to addressing landscape-matrix questions should integrate patch quality into the study of animal movement.

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