WHICH SPATIAL HETEROGENEITY FRAMEWORK? CONSEQUENCES FOR CONCLUSIONS ABOUT PATCHY POPULATION DISTRIBUTIONS

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Abstract. Patches, gradients, and hierarchies are three common organizational frameworks for assessing the effects of spatial heterogeneity on species distributions. Since these frameworks are often chosen a priori, without knowledge of study systems, they may not correspond to the empirical heterogeneity present and may result in partial or erroneous conclusions about the forces structuring species distributions. I tested the consequences of choosing particular frameworks and whether patch heterogeneity structured patchily distributed populations of the valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*) along four rivers in California's Central Valley (USA). A comparison of the three approaches revealed that each led to incomplete conclusions about controls on the beetle's distribution and populations. Patch analysis revealed weak effects of patch size and quality, and high unexplained variance, which likely reveals large amounts of stochasticity since replication was high. The patch analysis therefore concluded that distributions consistent with patch dynamic structures like classic metapopulation, source–sink, and mainland–island models existed in the different rivers. Conversely, gradient analyses revealed a gradient-distribution pattern responding to continuous and often large-scale variables, such as host-plant age or size, water availability, and the presence of an invasive leguminous tree; again most variance in beetle occurrence remained unexplained. Hierarchical analysis identified the natural spatial patterns of the system but gave no indication of causal processes. The combination of all three approaches explained the maximum variance in beetle occurrence, through inclusion of a comprehensive list of explanatory variables, multiple spatial scales, various types of heterogeneity, and a focus on the scales at which beetle–environment interactions were strongest. Surprisingly, these results still supported the notion that the beetle exists as a metapopulation, a structure thought to be rare because it ignores habitat quality and landscape conditions. These analyses exemplify the simultaneous importance of local patch attributes and broad-scale and/or gradient variables that are commonly overlooked in patch studies. Importantly, some patch attributes acted over inter-patch scales, affecting the perception of patch distances and distributional extents. Only through the integration of frameworks was I able to decipher the system's complexity and see that all three types of heterogeneity were acting in the system, sometimes over unexpected scales.

Key words: California's Central Valley (USA); Desmocerus californicus dimorphus; *gradient analysis; hierarchical analysis; metapopulation; patch analysis; patch dynamics; patchy populations; scaling; spatial heterogeneity; species distributions; valley elderberry longhorn beetle.*

INTRODUCTION

The influence of spatial heterogeneity on population and community structure has long been recognized in ecology (e.g., Cowles 1899, Gleason 1926, Clements and Shelford 1939). Ecologists have viewed spatial heterogeneity and its effects on species distributions using at least three different organizational frameworks: as a network of varying patches (e.g., Levins 1969, Wiens 1976, Hanski 1994*a*), as a gradient (Whittaker 1967, Dayton 1971, Keddy 1991), and as a hierarchy of processes acting over a variety of scales (Haury et al. 1978, Allen and Starr 1982, O'Neill et al. 1986). There is generally an a priori selection of these frameworks, usually based on limited knowledge and assumptions about the dominant types of heterogeneity in the system. The consequences of choosing the framework for one type of heterogeneity while another is dominant in the system, however, are seldom if ever considered although they may include erroneous or incomplete conclusions about the resulting species-distribution patterns or the forces structuring the distributions. These consequences will vary with the adopted and actual heterogeneity present in the system, as this study illustrates.

The spatial frameworks

Patch-dynamic theory, including classic metapopulation, mainland–island, and source–sink models, views systems as patches of habitat or populations embedded in a contrasting, uninhabitable matrix (Fig. 1A,
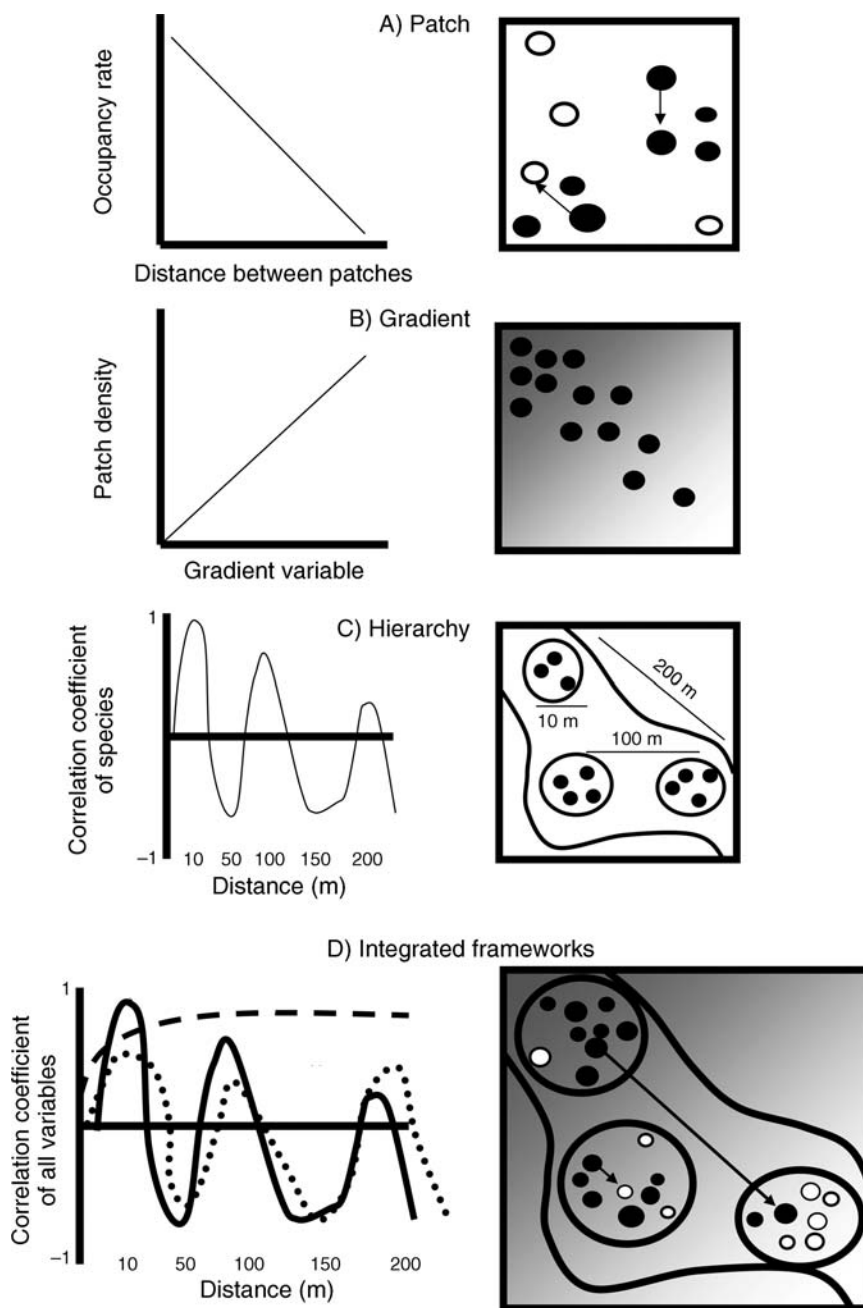
Fig. 1. Schematics of typical data graphs and ecosystem diagrams as viewed using the assumptions and approaches of each of the three common heterogeneity frameworks (A–C) and a representation of the combination of information when integrated (D). Black circles represent occupied patches, and white represents vacancy. Here, any of the individual approaches would not have captured all the processes at work structuring the species distribution. For example, occupancy not only declines with distance between patches (A), but also at the less optimal (lighter) end of the gradient (B); both processes can be seen in the integrated framework panel (D). While gradient and hierarchy analyses reveal linear and hierarchical distributions of the species, respectively, the patch approach is the only one to include vacant habitat. Hierarchy then reveals corresponding natural (not biased by researchers) structures of habitat patches and the species, suggesting no shortage of habitat despite higher differences in occupancy at the broadest scale.

diagram). A typical study may examine the roles of patch isolation, size and quality, and the importance of vacant patches in species-occupancy patterns (Hanski 1994a, Moilanen and Hanski 1998). The focus tends to be on fine (patch) scales, where patches are defined by the researcher, and overlooks variables related to the interpatch matrix or landscape and multiple scales (Fig. 1A, D).

Gradient theory views systems as gradients of variables over which species distributions or interactions may change (Fig. 1B). A typical study may explore the mechanisms for occupancy patterns, such as environmental tolerances of the species, as well as the interactions between tolerance and local biotic processes (Keddy 1991, Dayton 1994, Thrush et al. 2000). Gradients tend to focus on broad scales with little or no consideration of patch variables or how observed interactions or population dynamics change across scales (only across the gradient at a given scale; Fig. 1B, D).

Hierarchy theory views systems as mosaics of discrete, multiscale patches (Fig. 1C) within which processes operating on similar spatial and temporal scales occur, interacting little with processes in larger or smaller patches (Allen and Starr 1982). "Patches" usually refer to spatial aggregations of species or conditions (i.e., not determined by the researcher), and not distinct units of a population as in patch-dynamic theory. Although the theory is thought to be too formal to represent complex natural systems (O'Neill 2001), a hierarchical approach requires the useful identification of the spatial patterns of species or conditions (O'Neill et al. 1986, 1991). Spatial patterning provides insight into the scales at which important processes occur and how processes change with scale, but the identity of these processes is generally inferred from the spatial patterns. Furthermore, population dynamics and interactions between species and with the environment are usually overlooked (Fig. 1C, D).

Each approach provides unique spatial, environmental, and species information about the system and, used in combination, should present a more comprehensive view of a system (Fig. 1D).

Integration of approaches

Previous studies have integrated approaches, but often the focus is on what is learned by integrating spatial scales rather than exploring the relevance of different forms of heterogeneity (but see Thrush [1991]). This has resulted in the loss of useful information through neglect of the variables associated with the underlying theories and the heterogeneity patterns themselves. Patch and gradient approaches have been used in systems structured by large-scale physical gradients, such as deserts (Brown et al. 1979), coastal marine systems (Dayton and Tegner 1984, Hewitt et al. 1996, Thrush et al. 2000), and rivers (van Coller et al. 2000, Turner et al. 2004). Often, however, patches are grossly defined as small-scale areas (e.g., Forman 1995, Argov et al. 2003) instead of the areas within which local population dynamics occur (e.g., Hanski 1994b), thereby losing information.

Hierarchies have been combined with patch approaches (Kotliar and Wiens 1990, Wu and Loucks 1995) and gradients, such as where systems have multiple site-specific processes or gradients acting over different spatial scales (Hewitt et al. 1996, Pausas et al. 2003). Hierarchical studies often compared the effects of broad- and fine-scale processes (e.g., non-nested hierarchy analysis; Summerville and Crist 2004, Talley 2005). Less frequently they conducted cross-scale assessments of the same processes interacting and changing through space, which could reveal the scale-dependent effects of heterogeneity patterns on distributions (e.g., nested hierarchy; Allen and Hoekstra 1990, Hewitt et al. 1997, 2002, Thrush et al. 2000, Benedetti-Cecchi 2001, Cushman and McGarigal 2004).

My study illustrates that explicitly integrating these three heterogeneity frameworks can provide a more complete and accurate view of complex systems. Despite having a system that seemed obviously patchy, all forms of heterogeneity acted, often on unexpected scales.

Consequences and assumptions

I used an obviously patchily distributed empirical population to (1) test the consequences of using the patch-dynamic, gradient, and hierarchical frameworks for the conclusions drawn about the forces structuring the population, and (2) test whether patch heterogeneity was the dominant force structuring the population. The empirical example is the valley elderberry longhorn beetle (*Desmocerus californicus dimorphus* Fisher, Cerambycidae; see Plate 1), a federally threatened subspecies that is indigenous to California's Central Valley (USA) (USFWS 1980). This beetle completes all stages of its life cycle on shrubs of blue elderberry (*Sambucus mexicana*), a common riparian shrub. It is thought that shrubs, when large or somewhat isolated, or clusters of shrubs, serve as patches for the beetle (e.g., Barr 1991, Collinge et al. 2001). Any of these three frameworks could be applied to the beetle, and could therefore be reasonable approaches for determining controls on distribution patterns. These goals were met by testing the following predictions about the forces structuring beetle distributions based on the assumption that each type of heterogeneity was dominant in the system:

1) *Patch heterogeneity*. Since the beetle exists in low local densities, is dispersal limited, and is strongly associated with its patchily distributed host plant (Collinge et al. 2001, Talley 2005), isolation distance of occupied shrubs, and shrub/patch area and quality will influence occupancy of the beetle (e.g., MacArthur and Wilson 1967, Levins 1969, Pulliam 1988).

2) *Gradient heterogeneity*. Both the beetle and its host plant are riparian species, and rivers exhibit gradients of variables, such as flooding, water availability, and cover of woody vegetation (van Coller et al. 2000, Turner et al. 2004). These gradients will be correlated with beetle presence through effects on both the beetle and its host plant.

3) *Hierarchical structure*. Occupancy patterns of the beetle should be hierarchical with fine scale distributions related to host quality and mate detection and broad
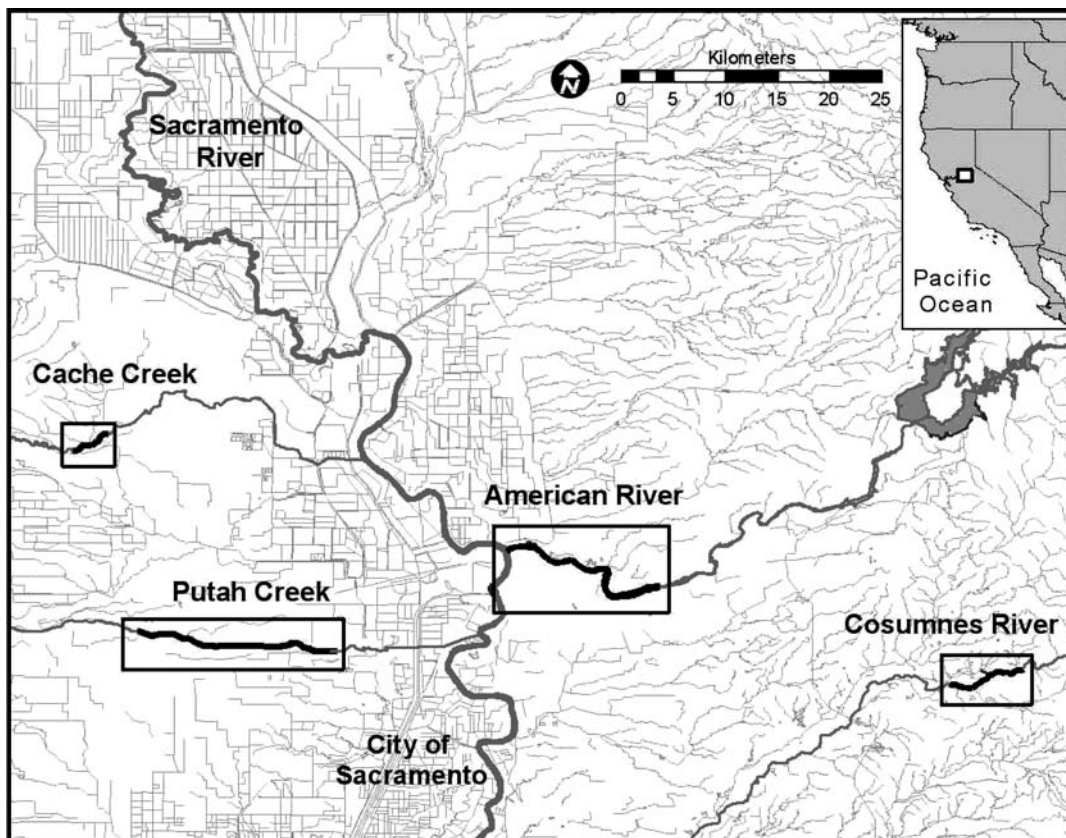
FIG. 2. Site map of the riparian study sites in California's Central Valley. Each study reach is a low gradient, alluvial river. (Map by A. K. Fremier.)

distributions corresponding with the distributional extent of its host, elderberry.

The comparison of these three approaches is, in part, a heuristic exercise. The variables selected for use in each framework were those expected to be important based on the related theory. An obviously important variable or scale would not, however, be excluded from a study just because the theory underlying the chosen framework does not explicitly account for it. Furthermore, each heterogeneity pattern is a somewhat arbitrary classification along continua of pattern intensity, which describes distributions of density from random to aggregated, and form, which describes the spatial extent of pattern (Thrush 1991). There are studies, however, that have taken advantage of the simplification that these frameworks offer to explain or predict species distributions or regional population persistence (e.g., O'Neill et al. 1991, Hanski 1994a, Hill et al. 1996, Frank 2005). A comparison of the outcomes of the three approaches is therefore useful. These predictions were tested using spatially extensive, well-replicated data sets that were collected over a period of two years (2002–2004). An integration of both field surveys and GIS provided variables used in the three analyses.

METHODS

Study sites

Four rivers in California's Central Valley (USA) were surveyed to encompass the variability in conditions throughout the northern portion of the beetle's range. Sites consisted of a 24-km reach of the Lower American River (3384 shrubs; Sacramento County, California), three reaches totaling 28 km of Putah Creek (1152 shrubs; Yolo and Solano Counties), 2 km of Cache Creek (219 shrubs; Yolo County), and 3 km along the Cosumnes River (189 shrubs; Sacramento County) (Fig. 2). The three reaches along Putah Creek, from downstream to upstream, were 13, 6.5, and 8.5 km long, and were separated, respectively, by 8.5-km and 4.5-km inaccessible reaches. The scales examined along Putah Creek ($\leq$1.5–3 km) were smaller than the length of the inaccessible reaches, which therefore did not likely affect the analyses. Furthermore, elderberry was limited in these gaps. Although relatively short in river length, the Cache Creek and Cosumnes reaches had floodplains that were relatively wide (0.5–0.75 km, 0.3–0.5 km respectively) allowing for examination of beetle spatial distributions on <0.6-km scales. Sites along these rivers were selected because of accessibility (i.e., public property) and because they have vegetation assemblages

and land-use types that are typical of riparian corridors, and therefore beetle habitat. The inaccessible areas surrounding the sampled reaches often had little to no elderberry visible and tended to be cleared agricultural lands, developed residential areas, or steep rocky terrain.

Although all four rivers have invasive, exotic plants present, the American River has the most extensive invasion of black locust (*Robinia pseudoacacia*), a nitrogen-fixing tree that favors the same open, moist conditions as elderberry (5% of points surveyed on the American River vs. 0–0.1% along other rivers). Surveys were conducted in spring and summer 2002–2004.

Data collection

Sampling was spatially continuous, with every elderberry shrub growing within each site (river reach) being sampled. Elderberry grows vegetatively from underground shoots, therefore a shrub was defined as a cluster of main stems growing ≤10 m apart from each other. This distance was based on field observations of maximum rhizome lengths. For each and every shrub, all variables were measured in the field or calculated using GIS, with the exception of the nutrient data which were collected from a subset of shrubs as is described in *Host-plant quality*, below.

Field measurements.—Geographic coordinates, maximum basal stem diameter, total number of main stems per shrub, number of beetle exit holes, and percent cover of canopy and canopy species were recorded using a GPS receiver (accuracy: 1 m) at each elderberry shrub. Canopy cover was visually estimated as the percentage of tree canopy covering the elderberry shrub canopy. For elderberry shrubs with a canopy diameter ≥5 m, area was measured by creating a polygon around the drip line of the shrub with a GPS receiver. A linear regression of stems per shrub (canopy diameter ≥5 m) vs. area was used to estimate the areas of abundant, smaller shrubs (diameter <5 m) using the number of stems from those smaller shrubs. A subsample of the area estimates made using this regression function were successfully field validated.

Beetle emergence holes are used to survey populations of this spatially and temporally rare species (Barr 1991, Collinge et al. 2001). While adult beetles live for only a few weeks in the spring, during which they feed on elderberry leaves and flowers, the larvae develop for 1–2 years, feeding on pith at the center of stems (Linsley and Chemsak 1972). The fifth-instar larvae create exit holes in the stems, then plug the holes and remain in the stems through pupation. Adults emerge in the spring through the distinctive exit holes. Recent holes had crisp margins, minimal evidence of healing, light-gray wood, and, in some cases, frass (wood shavings and droppings). The beetle is the only species that creates appropriately sized holes in live elderberry in this region (Barr 1991).

Host-plant quality.—Percentage nitrogen content of elderberry pith and leaves was measured for 25–480

shrubs within each reach. Shrubs were chosen based on distribution across the study area, and by ensuring that 50–100% of occupied shrubs and at least as many unoccupied shrubs were sampled. Analyses in which nitrogen was a significant variable, therefore had much reduced replication (e.g., American River, Tables 2–4). In each of those cases, however, the presence of the N variable increased the amount of explained variance over the analysis in its absence, despite the lower replication. At least 10 green, uninjured leaves were collected from each shrub and, along the American River and Putah Creek, a 25–30 cm long section of 1.5–2 cm diameter stem was also collected from each shrub. Plant material was kept frozen at −30°C until analysis. In the laboratory, pith was extracted from the surrounding woody portion of stem, and both the pith and leaves were rinsed with deionized water, completely dried at 65°C, finely ground, and analyzed for percentage N content using combustion (DANR 2005). Nitrogen content of pith and leaves were correlated ($R^2 = 0.24$, $P < 0.001$, $F_{1, 232} = 73$) and both were associated with beetle abundance along the American River and Putah Creek, but pith N content had stronger relationships so was used in the analyses for these rivers. The weaker effect of leaf N may in part explain the lack of observed effect on beetle abundance in Cache Creek and the Cosumnes River.

Spatial calculations.—The shortest distances from each and every elderberry shrub to the nearest recently occupied shrub or aggregation (see *Spatial structures*, below) were calculated using the Nearest Features script for ArcView 3.2 (ESRI 2004*b*, Jenness 2004). Shrub densities were estimated within discrete areas of 1963 m^2 (a 25-m-radius circle) using ArcGIS 9.0 (ESRI 2004*a*) neighborhood statistics. Relative elevation was calculated for each shrub using 30-m digital elevation models (CaSIL 2000) and was the difference between the elevation (in meters above sea level) at the shrub and the elevation of the surface of the river nearest to the shrub. The use of 30-m elevation models in these areas that have relatively little elevational variation (≤37-m elevational variation) may underestimate the effects of elevation. The few but significant relationships between beetle occupancy/abundance and relative elevation indicated, therefore, that fine-scale elevational changes may be important to the beetle and should be explored further.

Statistics

Relationships between independent variables.—All independent variables were log_{10}-transformed (or arcsine square-root transformed for proportions) before analyses to normalize data and ensure homogeneity of variance. Relationships between independent variables within each analysis (patch, gradient) were explored using Pearson's correlations and simple linear regressions (JMP 2005). If relationships were significant ($P < 0.05$ and $R^2 > 0.1$), then only the most ecologically
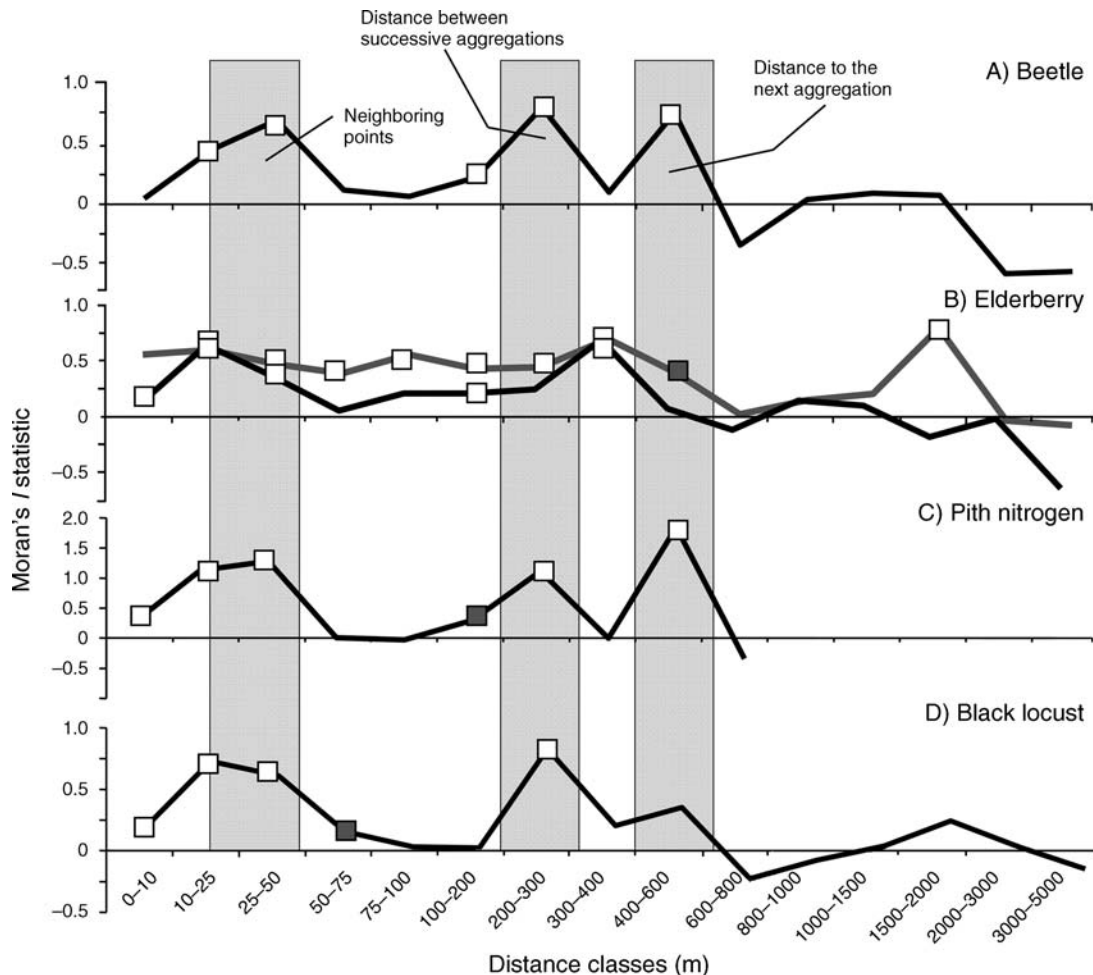
FIG. 3. Correlograms showing the hierarchical levels of spatial clustering along the American River of (A) populations of the valley elderberry longhorn beetle, and of those variables found to be significantly associated with the beetle: (B) area and maximum basal diameter (gray line) of the beetle's host plant, elderberry, (C) percentage nitrogen content of elderberry pith, and (D) cover of the invasive nitrogen-fixing tree, black locust. Gray bars highlight any overlap in scales of beetle population aggregations and the environmental variables. White symbols indicate $p \leq 0.01$, gray symbols indicate $0.01 < p \leq 0.05$, and no symbol indicates $p > 0.05$; $n = 64$ aggregations (patches) at 25 m, 13 at 200 m, and 11 at 400 m. Labels explaining correlogram of patchy distribution in graph (A) are adapted from Legendre and Fortin (1989); distribution of maximum diameter in graph (B) is that of a gradient (Legendre and Fortin 1989).

sensible variable was used or the residuals of the regression between the two co-linear variables were used instead of the more ecologically dependent environmental variables (Graham 2003). Independent variables used in the gradient analysis were also spatially detrended by removing effects of latitude and longitude through use of the residuals. Linearity of relationships between the dependent (beetle occupancy or abundance) and independent (environmental) variables was tested using simple regressions in JMP.

Spatial structure.—The spatial structure of the beetle and independent (environmental) variables was explored in ArcGIS 9 (ESRI 2004b) using Moran's *I* test for spatial autocorrelation calculated across a range of distance intervals (see Fig. 3 for distance intervals used). Moran's *I* statistic ranges from about −1 to 1. Values

approaching 1 indicate positive spatial autocorrelation (clustering), those approaching −1 indicate an even distribution, and those around 0 indicate no pattern. A peak of autocorrelation was considered an "aggregation" if Moran's $I \geq 0.50$ and $P \leq 0.05$.

Patch and gradient analyses.—Backward, stepwise, multiple logistic regressions were used to assess the relationships between beetle occupancy of shrubs (dependent variable) and environmental variables in the patch-dynamic and gradient analyses (Table 1). The independent variables consisted of characteristics of the patch, defined as the host shrub, and characteristics of the landscape between or outside of patches, or shrubs. The independent variables used in the patch-dynamic approach were those emphasized in patch-dynamic theory: patch size (shrub area), patch quality (shrub N

TABLE 1. The parameters used to test each of the spatial-heterogeneity frameworks.

Type of parameter	Spatial-heterogeneity framework		
	Patch	Gradient	Hierarchy
Ecological unit	shrub = patch	shrub	aggregation
Independent variables	area	diameter	diameter/area
	quality (nitrogen)	quality (nitrogen)	quality (nitrogen)
	distance to next occupied patch	density	distance to next occupied aggregation
		canopy cover	shrub density
		relative elevation	canopy cover
			relative elevation
Response variable	occupancy	occupancy	abundance (including 0's)
Statistical test	logistic multiple regression	logistic multiple regression	linear multiple regression

content) and isolation (distance to nearest occupied shrub; Table 1). The gradient analyses used independent variables that were likely direct resultants of association with a river (relative elevation) and those influenced by this physical gradient (Table 1) as based on literature (e.g., Naiman and Decamps 1997, Turner et al. 2004) and exploratory analyses.

Hierarchical analysis.—The hierarchy analyses used habitat variables with a similar spatial structure to the beetle based on Moran's *I* (Fig. 3), and those found important in the other analyses (Table 1), since hierarchy theory does not emphasize particular types of variables. Beetle population aggregations were identified using Moran's *I* and used as the units of replication (vs. individual occupied shrubs; e.g., Jax et al. 1998) in the hierarchical analyses. Aggregations, or habitat patches, at each scale were created in ArcGIS 9 by drawing Thiessien's polygons around groups of elderberry shrubs that occurred within the distance intervals of each other shown in Fig. 3. Variables were either summed (e.g., number of shrubs to calculate density), averaged (e.g., plant quality) or recalculated (e.g., distance between occupied aggregations) as appropriate within these polygons and backwards stepwise linear multiple regressions were used to test for relationships between beetle abundance in aggregations and the environmental variables (Table 1) (e.g., Hewitt et al. 1997). Sequential Bonferroni adjusted alpha values were used to assess significance of relationships within rivers.

Between-river differences.—There were significant interaction terms between river and most of the covariates (the independent variables used in the analyses) as determined by general linearized models (JMP). This violates the assumption of homogeneity of slopes needed for ANCOVA, which was therefore avoided. All analyses were therefore carried out within rivers.

RESULTS

The heterogeneity frameworks

Patch-dynamic framework.—Along the American River, connectivity of patches (decreased distance) and increased shrub quality (percentage nitrogen content) had the largest effect on beetle occupancy (Table 2). Patch, or shrub, area was positively associated with occupancy in both Putah Creek and the Cosumnes River (Table 2). Occupancy was additionally positively associated with decreased connectivity (increased isolation) along the Cosumnes (Table 2). No factors significantly explained occupancy of shrubs in Cache Creek and only low amounts of variance in beetle occupancy ($\leq$11%) were explained by independent patch variables in all systems (Table 2). The well-replicated, spatially extensive data set makes it unlikely that a lack of statistical power was responsible for most of the unexplained variance, suggesting that variables overlooked in this analysis and/or stochasticity played a role in beetle occupancy in all systems (e.g., Bonsall and Hastings 2004).

Gradient analyses.—Occupancy in all rivers depended primarily on a gradient of the maximum basal diameter of shrubs (Table 3), which reflects both shrub size and

TABLE 2. Results of the patch-dynamic analysis along the study sites in California's Central Valley, USA.

River	Important variable†	R^2	P	χ^2	N‡	df	Possible conclusion§
American River	+ connectivity + shrub quality (%N)	0.08	<0.0001	22	248	2	classic metapopulation and source–sink
Putah Creek	+ shrub area	0.07	<0.0001	26	1152	1	mainland–island
Cache Creek‖	none		NS		218		classic metapopulation
Cosumnes River	+ shrub area − connectivity	0.11	0.03	7	189	2	mainland–island, no independent effects of isolation

† The "+" and "−" symbols denote the direction of the relationship between the independent variable and beetle occupancy.
‡ Sample size, i.e., number of elderberry shrubs.
§ Based on patch theory, some possible, not necessarily correct, conclusions about population structure that may be drawn based on the variables found to be important in the analyses.
‖ Blank cells indicate not applicable because the test was not significant (NS).

TABLE 3. Results of the gradient analysis.

River	Important variables†	R^2	P	χ^2	N	df	Possible conclusion‡
American River	maximum diameter (+0.12) shrub quality (%N) (+0.02) black locust cover (+0.05) relative elevation (−0.02)	0.22	<0.0001	127	714	4	occupancy depends mostly on small-scale gradients of shrub size and quality, and secondarily on landscape gradients
Putah Creek	+ maximum diameter	0.06	<0.0001	34	1152	1	occupancy depends on shrub-size gradients
Cache Creek	+ maximum diameter	0.04	0.04	4	218	1	occupancy depends on shrub-size gradients
Cosumnes River	+ maximum diameter	0.25	<0.0001	17	188	1	occupancy depends on shrub-size gradients

† The "+" and "−" symbols denote the direction of the relationship between the independent variable and beetle occupancy; maximum diameter is the shrub maximum basal diameter, %N indicates percentage nitrogen content, and r values for the American River are shown in parentheses.

‡ Based on gradient theory, some possible, not necessarily correct, conclusions about population structure that may be drawn based on the variables found to be important in the analytses.

age. Increased shrub quality, cover of invasive black locust tree, and decreased relative elevation (greater access to soil moisture) increased the chance of occupancy along the American River (Table 3), but not along the other rivers. Gradient analysis explained 2 to 4 times more of the variance in beetle occupancy than the patch analysis in three rivers and similar amounts of variance along Putah Creek. The weak or undetected effects of landscape gradients on beetle occupancy could be interpreted as indirect effects of gradient properties affecting the host-plant elderberry (Talley 2005), which in turn would affect beetle.

Hierarchical analysis.—

1. *Beetle distributions.*—Spatial autocorrelation analysis of beetle populations revealed no distributional patterns along Cache Creek (Moran's I between −0.3 to 0.2, $P \geq 0.1$), and two hierarchical levels of patches along the other three rivers (only the results of the American River are illustrated; Fig. 3). Local aggregations covering 25–50 m scales occurred at distances of 200–300 m along the American River (Fig. 3) and 600–800 m apart along Putah Creek (Legendre and Fortin [1989] interpret the shapes of correlograms). The extent of each group of aggregations was ~800 m along the American River (Fig. 3) and up to several kilometers along Putah Creek. Aggregations along the Cosumnes were more spread out (200–300 m) and were separated by 400–600 m distances, which was about the extent of the distribution in the area sampled.

2. *The natural patterns of environmental variables.*—Despite my initial assignment of all variables as patch or gradient, their natural spatial structure varied as revealed by hierarchy analysis. In all rivers, relative elevation existed as a gradient (Legendre and Fortin 1989), while shrub area and quality, and cover of black locust canopy exhibited patchy distributions (Fig. 3; Table 4). Correlograms of only those variables significantly related to beetle occurrence in aggregations along the American River are shown (Fig. 3). Shrub density and maximum stem diameter (shrub size and age) exhibited different types of heterogeneity among rivers and consisted of large or small patch or gradient structures (Table 4). For example, maximum stem diameter formed gradients or patches across rivers

and, along the American River, formed gradients over 300–400 m scales that repeated every 1.5–2 km (i.e., large patches of gradients; Fig. 3).

3. *Multi-scale environmental effects on the beetle.*—In general, gradient and/or patch variables reflecting elderberry availability (shrub density, shrub area, and maximum stem diameter) primarily affected beetle occupancy across all scales along three of the four rivers, but the additional contribution from other environmental variables varied with river and scale (Table 4). Along the American River, a complex nested hierarchy emerged: gradients of maximum shrub diameter (shrub size and age) and patches of black locust affected local beetle aggregations (25–50 m) and their distributions (200–300 m) (Fig. 3, Table 4). Patches of shrub quality also influenced local-scale aggregations along with the distributional extent of aggregations (~800 m), which was additionally influenced by smaller shrubs areas (Fig. 3, Table 4). The least amount of variance in beetle occurrence was explained at the intermediate scales (17% vs. 59–61% at other scales), indicating the influence of an unmeasured factor or a larger role of stochasticity acting on aggregation distances.

Beetle distribution across all scales along Putah Creek was influenced primarily by gradients in shrub density and connectivity (or isolation) of beetle aggregations (Table 4). Patches of shrub size/age and quality additionally contributed to the extent of aggregations (1.5–3 km). Shrub availability and isolation of the beetle explained only 9% of the variance in local beetle aggregations (25–50 m) compared with 59–78% of variance explained for the distributional extent of aggregations, indicating, again, an unmeasured variable or large role of stochasticity acting on the small scale.

Occupancy and distribution of aggregations along the Cosumnes River was influenced by patches of shrub density and the gradient of water availability (relative elevation) (Table 4).

Contribution of each form of heterogeneity

The patch-dynamic approach explained ≤11% of the variability in beetle occupancy (Table 2) along all rivers. The gradient approach explained 4–25% of the variabil-

TABLE 4. Results of the hierarchical analysis, by river; values are results of backward stepwise multiple linear regressions performed between environmental variables and beetle abundance within each distance interval.

Scales of beetle distribution[†]	Shrub				Dist. to occupied[‡]	Black locust cover	Relative elevation[§]
	Area	Max. basal diameter	Density	Quality (%N)			
American River	P	G	G	P		P	G
25–50 m	NS	+0.42	NS	+0.09	NS	+0.07	NS
200–300 m	NS	+0.11	NS	NS	NS	+0.05	NS
400–600 m	−0.30	NS	NS	+0.31	NS	NS	NS
600–800 m	n.a.						
1.5–3 km	n.a.						
Putah Creek	P	P	G	P		φ	G
25–30 m	NS	NS	+0.05	NS	−0.04	NS	NS
200–300 m	n.a.						
400–600 m	n.a.						
600–800 m	NS	NS	+0.28	NS	−0.31	NS	NS
1.5–3 km	NS	+0.12	+0.31	+0.09	−0.16	NS	NS
Cache Creek¶	P	φ	G	P		φ	G
Cosumnes River	P	P	P	P		φ	G
25–50 m	n.a.						
200–300 m	NS	NS	+0.20	NS	NS	NS	−0.16
400–600 m	NS	NS	+0.11	NS	NS	NS	−0.87
600–800 m	n.a.						
1.5–3 km	n.a.						

Notes: Values are the results of backwards, stepwise, multiple linear regressions performed between environmental variables and beetle abundance within each distance interval. Data are r^2 values, with the direction of the relationship denoted by + or −, and the result of each whole regression model: NS = not significant (P < sequential Bonferroni-adjusted α of 0.10); n.a. = not applicable to that river; P = patch structure, G = gradient structure, and φ = no detectable pattern. Different relationships across scales indicate a hierarchical structure.

† Distance intervals correspond with spatial aggregations of the beetle along that river.

‡ Distance to nearest occupied aggregation or patch.

§ The difference between the elevation (in meters above sea level) at the shrub and the elevation of the surface of the river nearest the shrub.

|| Sample size.

¶ No hierarchical spatial patterns. If a larger area could have been surveyed, broad-scale hierarchical patterns could possibly have been observed.

ity, with improvement over the patch approach in all but one river (Tables 3 and 4). Additionally, only a gradient approach significantly explained any variance in occupancy along Cache Creek, which lacked a population distribution pattern. The hierarchy analysis explained the most variance in beetle occupancy (average of 46–66%) for the three rivers where beetle spatial structure was observed (Table 4); this was calculated by averaging R^2 values across hierarchical aggregations within rivers.

DISCUSSION

Consequences of adopting each spatial framework

Patch framework.—With a patch approach, the variables important to population structure included some combination of isolation, stochasticity, and donor patches (e.g., larger area, better quality) resulting in structures consistent with mainland–island, source–sink, and classic metapopulation models (Levins 1969, Boorman and Levitt 1973, Pulliam 1988). Relationships were weak, however, increasing the possibility of other forces at work. The weak associations between the beetle (*Desmocerus californicus dimorphus* Fisher, the valley elderberry longhorn beetle) and patch size and quality could have been due in part to the covariance of these variables with unmeasured gradients (Table 5). Additionally, exclusion of gradient or other among-patch variables or scales may have contributed to unexplained variance. The significance of variables in the gradient analysis supports this interpretation. Similarly, the adoption of a patch framework, when the species and environment had a hierarchical structure, often led to the erroneous designation of patch extent (Table 5). The hierarchical approach revealed fine-scale spatial autocorrelation in three of the rivers, indicating that groups of shrubs and not individual shrubs often comprise habitat patches. This is important information when applying patch theories or models, which assume patches to be independent entities.

Gradient framework.—The gradient analysis revealed the potential role of continuous, broad temporal- and spatial-scale habitat and landscape properties (e.g., shrub age, black locust cover, relative elevation) in structuring populations. These types of variables are not traditionally included in patch analyses. Again, however, relationships were weak, suggesting influence of more than just the observed gradients. Weak relationships between the species and gradient might be explained by a lack of effect of the gradient variable or the assumption that the real contributing factor or important scale (e.g., Legendre et al. 1997) was overlooked

TABLE 4. Extended.

R^2	P	F	$N\|$	df	Conclusion
		Statistics			
					gradient-influenced patch hierarchy
0.59	<0.0001	29	64	3, 60	
0.17	<0.0001	17	173	2, 170	
0.61	0.022	6	11	2, 8	
					gradient-influenced patch hierarchy
0.09	<0.0001	29	596	2, 593	
0.59	<0.0001	31	47	2, 44	
0.78	0.005	8	14	4, 9	
					classic metapopulation (within the scales examined)
					gradient-influenced patch hierarchy
0.36	0.10	3	13	2, 10	
0.95	0.01	27	6	2, 3	

(Table 5). If the "real" heterogeneity structure is that of patches, then stochasticity and isolation could cause areas to be unoccupied and disrupt detection of observed relationships with the environment (Table 5). Similarly, a hierarchical heterogeneity pattern that did not correspond with the assumed gradient could cause species–gradient relationships to appear stronger (e.g., via autocorrelation) or weaker (e.g., by confounding patterns) than in reality (Table 5).

Hierarchical framework.—The improved explanatory ability of the hierarchy analysis over the patch and gradient analyses indicated that the interactions between beetle occupancy and the environment varied with scale (e.g., Legendre et al. 1997, Wu et al. 2000) and were

TABLE 5. Consequences of adopting a spatial-heterogeneity framework that does not correspond with the type of heterogeneity in the system of interest.

Adopted framework	Empirical heterogeneity		
	Patch	Gradient	Hierarchy
Patch	can consider effects of patch quality, size, isolation, and stochasticity highlights value of vacant habitat researcher defines patch extents, which may not be accurate	distributions due to fitness trade-offs along a gradient may be falsely attributed to patch vacancy or regional population extent caused by stochasticity or isolation perceived patches may not be independent if influenced by underlying gradient may assume donor patches when gradient is affecting distribution	may falsely define patch or metapopulation extent so recorded occupancy is meaningless may miss changes in distribution or interactions across spatial scales
Gradient	may assume gradient effects (or no effects) when patch occupancy patterns are due to stochasticity or isolation may assume that unmeasured factors along the gradient account for occupancy patterns	reveals processes explaining distribution patterns (e.g., fitness trade-offs, environmental tolerance) reveals causes of autocorrelation in distributions researcher defines gradient extent, which may not be accurate	important and/or nested spatial scales may be ignored gradient may not correspond with hierarchical patterns to reveal causes of distribution
Hierarchy	may conclude non-hierarchical patterns if distribution is due to stochasticity or isolation hierarchical patterns may not explain small-scale movements, which are independent of habitat may help to define spatial extent of patches a priori	hierarchical structure may vary across gradients may miss process underlying hierarchical pattern if gradient is ignored if discontinuous gradient, may assume processes are acting over smaller scales than they really are	reveals important scales and whether processes transfer across scales study system defines appropriate scales and structures (e.g., patches)

Note: Species distributions = occupancy and abundance.

PLATE 1. (Left) Adult male (top) and female of the federally threatened valley elderberry longhorn beetle (*Desmocerus californicus dimorphus* Fisher) mating on a leaf of the host shrub, elderberry (*Sambucus mexicana*). (Right) Adult male valley elderberry longhorn beetle. Beetles are about 1.5 cm from head to posterior tip of elytra. Photo credit: T. S. Talley.

often the results of both cross-scale processes (a mix of broad- and fine-scale variables) and environmental variables displaying different types of heterogeneity. In general, the beetle populations exhibited a hierarchical patch structure with two levels of aggregation, local and regional. In Cache Creek, however, the beetle's distribution had no significant patterning, which is consistent with a classic metapopulation structure with shrubs as patches. Assuming a hierarchical structure in this case could have led to an erroneous designation of population extent, which was not observed within this relatively small area surveyed (Tables 4 and 5). Additionally, observed changes in hierarchical structure across scales could be due to gradient-induced changes in species distribution. For example, species may use larger habitat areas in lower-quality regions (Schoener 1989). If gradients remain overlooked, then the processes causing observed distribution patterns might be mis- or unidentified (Table 5). On its own, the hierarchy approach revealed unbiased spatial patterning of the system, including the potentially important scales of interaction and heterogeneity structure, revealing that our initial assumptions about structure were sometimes erroneous. Insights about the important variables and processes contributing to distribution patterns, however, came from the other analyses.

What integration revealed about the beetle's population distribution

Exploration across types of heterogeneity and spatial scales has revealed characteristics that are most consistent with a patch-dynamic structure. The beetle has regional distributions composed of local aggregations, both of which are influenced by habitat patch characteristics such as size, quality, connectivity, and stochasticity, as was expected by patch-dynamic theories. These integrative analyses revealed, however, that local aggregations often span multiple shrubs and that controls on both local aggregations and their distributions include

broader-scale and/or continuous factors, such as host age or densities, and riparian-associated environmental variables (relative elevation, associated trees). This reveals that the beetle's population predominantly has a patch-dynamic structure, as was suspected, but that controls on that structure include broad- and cross-scale processes reflecting all forms of heterogeneity (patchy, gradient, hierarchical)—all variables not considered with a patch approach.

Only through the simultaneous examination of multiple spatial scales did this study reveal the importance of cross-scale and scale-specific processes in influencing beetle distributions (e.g., Hewitt et al. 1997, Thrush et al. 2000, Cushman and McGarigal 2004). Variables often thought of as local controls, such as host-plant quality, affected distributions over fine (25–50 m) and broad (400–1500 m) scales, while traditionally broad-scale variables, such as relative-elevation gradients and isolation, sometimes affected distribution over smaller scales (<200–300 m). Integration of scales was needed to detect scale-dependent processes, such as beetle responses to host plant quality, and changes in processes across scales, such as a reversal in the beetle's association with larger shrubs from fine to broad scales. Cross-scale examinations are also likely to reveal interactions among scales that may result in emergent properties and contribute to system complexity (O'Neill et al. 1986).

Type of spatial heterogeneity

Each type of heterogeneity is often associated with particular scales, but this is not always the case. In this study, gradients were broad scale, as expected, but also fine scale. For example, relative-elevation gradients spanned several kilometers along the American River and only 75–100 m on the Cosumnes River, and shrub-density gradients covered 50–75 m scales on Putah and Cache Creeks. Additionally, patches were not necessarily the smallest structures, such as along Cache Creek

where patches of similar shrub areas spanned 200–300 m. Besides the role of multiscale processes in structuring distributions, the types of heterogeneity (e.g., patch, gradient, and hierarchical structures) may be important for several reasons.

The type of heterogeneity of the variables important to a species affects how the species moves and is distributed, and the nature of the variables can thereby reveal processes (Thrush 1991). For instance, the local patchy structure of the beetle corresponded with local patches of host plant quality, size and number, and/or small gradients in host-plant size and number. Processes explaining local beetle distributions therefore included the availability of particular values of host-plant quantity and quality (i.e., patches), or, in the case of the small gradients, the availability of a particular range of host attributes either because all values are similarly suitable or because heterogeneity in that variable is suitable.

The type of heterogeneity may also affect how the system or the species responds to external forces. Patch structures may be more prone to edge effects, and be less connected and more independent of each other than sites along a continuous gradient (e.g., Haddad and Baum 1999). These characteristics could affect habitat quality or the synchrony of the species life cycle and, therefore, responses to environmental fluctuations and movements of beneficial or detrimental organisms (Thomas et al. 1996).

Lastly, as mentioned earlier, the type of heterogeneity influences our assumptions about a system, the conclusions we draw about important structural forces, and the approaches we use to study the system. A variable with a gradient structure may require different measurements to capture variability than one with a patch structure. For all these reasons, we want to be sure we have correctly identified the types of heterogeneity and the scales over which they occur.

Explanations for population distribution

For many species, explanations for population distribution include not only environmental and spatial variables but also aspects of the species life history and individual behavior (Thrush 1991, Sih et al. 2004, and references in each). The several-hundred-meter distances between local aggregations supports the thought that the beetle, like related taxa (Gullan and Cranston 2004), has limited migration distances (USFWS 1984, Barr 1991, Collinge et al. 2001). Clustering of the beetle at the smallest scales (tens of meters) may be due to aggregation behaviors that are somewhat decoupled from the environment and that do not scale up to larger distances, such as detection of host-plant volatiles ($\leq$100-m scales) and conspecific (mate) attraction (centimeter scales) (e.g., Leal et al. 1995, Hanks 1999, Morales and Ellner 2002). The small local population size and low mobility of the beetle make influences of demographic and local environmental stochasticity likely. Therefore, both behavior and stochasticity can

affect distributions and weaken observed effects of environmental variables.

Ecological and conservation implications

This study revealed the potential complexity of natural systems, with the distribution of this rare habitat-specialist beetle dependent on three different forms of spatial heterogeneity, all variably acting across spatial scales and locations, and its individual behavior and natural history. The integration of these three common heterogeneity frameworks has been missing from ecological studies but is useful for identifying patterns, underlying processes, and, therefore, generalizations about the controls on species distributions, even if the distributions and species requirements seem obvious. A narrow view of the system, such as a focus on too few or the wrong spatial scales or types of heterogeneity, can lead to erroneous or incomplete conclusions and can obscure generalities.

Since ecological theory is the basis of ecological application, it follows that erroneous conclusions and a lack of generalities can lead to ineffective or deleterious conservation actions. The population structure of this elderberry specialist has, like many other rare specialist species, been assumed to be closest to a metapopulation (Collinge et al. 2001); a regional population composed of discrete patches with low occupancy rates, small local population sizes, and occasional colonization and extinction events (Levins 1969, Hanski 1994b). In addition, specialist species are assumed to have few but strong habitat requirements. These simple assumptions underpin the management of these species, which includes the use of metapopulation viability models (Possingham et al. 1994, Lindenmayer and Lacy 1995, Sjögren-Gulve and Hanski 2000). These models are thought to be too simplified to reflect the complexity of natural systems and therefore have low predictive ability (Harrison and Bruna 1999). We see from this study that the inclusion of multiple scales and types of heterogeneity (or pattern form and intensity) may allow these models to better explain natural variability and predict future outcomes.

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