

SPECIAL APPLIED ISSUES SECTION

Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams

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SUMMARY

1. Rapidly advancing geographical information systems (GIS) technologies are forcing a careful evaluation of the roles and biases of landscape and traditional site-based perspectives on assessments of aquatic communities. Viewing the world at very different scales can lead to seeming contradictions about the nature of specific ecological systems. In the case of Michigan trout streams, landscape analyses suggest a predictable community shaped by large-scale patterns in hydrology and geology. Most site-based studies, however, suggest these communities are highly variable in structure over time, and are strongly shaped by site-specific physical and biological dynamics. As the real world is comprised of processes operating both at local and landscape scales, an analytical framework for integrating these paradigms is desirable.
2. Decomposition of variances by factorial ANOVA into time, space and time–space interaction terms can provide a conceptual and analytical model for integrating processes operating at landscape and local scales. Using this approach, long-term data sets were examined for three insects and two fishes common in Michigan trout streams. Each taxon had a unique variance structure, and the observed variance structure was highly dependent upon sample size.
3. Both spatially extensive designs with little sampling over time (typical of many GIS studies) and temporally extensive designs with little or no spatial sampling (typical of population and community studies), are biased in terms of their view of the relative importance of local and landscape factors. The necessary, but in many cases costly, solution is to develop and analyse data sets that are both spatially and temporally extensive.

Introduction

Driven by rapidly developing geographical information systems (GIS) technologies (e.g. Goodchild, Parks & Steyart, 1993; Sample, 1994; Poiani & Bedford, 1995; and see Johnson & Gage, this volume), landscape-

scale analysis represents an exciting, if not altogether new, paradigm for understanding aquatic ecosystems, communities and populations. Integrating landscape-based perspectives with years of site-based data

gathering and theory, however, is for ecologists an important and substantial challenge. This is particularly true when considering the utility of landscape analysis in studies of population and community dynamics, which have traditionally focused on small-scale field experiments and data from a small set (frequently a single locale) of representative 'study sites'. The fundamental problem in this regard is that ecologists studying local aquatic populations, and ecologists employing GIS to examine ecological data from a landscape perspective, necessarily view the world at distinctly different spatial and temporal scales. Differences in perspective and scale often lead to an emphasis on different types of functional mechanisms (e.g. abiotic *v* biotic); processes operating at different rates (e.g. decades and centuries *v* days and weeks); and may require different modelling techniques (e.g. multivariate statistics *v* differential equations). Most importantly, these divergent perspectives can lead to divergent hypotheses and conclusions about both the structure and function of ecological systems (Ricklefs, 1987; Frost *et al.*, 1988; Wootton, 1992; Root & Schneider, 1995).

Most ecologists agree that in the real world both local and large-scale (regional) mechanisms are important (e.g. Schoener, 1983; Ricklefs, 1987; Pimm, 1991; Root & Schneider, 1995). But the question remains: How do we structure a comprehensive analysis? This paper examines some potentially conflicting conclusions about the nature of Michigan trout stream communities, which arise when comparing the results of current landscape and site-based studies. A simple decomposition of variance approach is described and employed to illustrate how these contrasting views might be reconciled. By way of example, two long-term data sets from Michigan streams are analysed and the spatial and temporal components of variation are estimated for a representative group of trout-stream taxa. Finally, based on this analysis, several important scale-related issues are discussed which face workers engaged in both GIS-based, and more traditional, site-based studies of lotic community structure.

Landscape and local constraints in Michigan trout stream communities

Hydrological and thermal characteristics of streams are strongly influenced by large-scale geological and

climatic variables. These lend themselves easily to GIS-based analyses. Michigan trout streams are cooled, and their flow stabilized, by large inputs of groundwater associated with deep deposits of glacial drift (see Fig. 1a). Outwash deposits provide exceptionally high hydraulic conductivities, which in conjunction with elevation head differences supplied by adjacent moraines can provide high rates of groundwater input to fortuitously located channel segments. As the landscape is a complex mosaic of different kinds of glacial deposits (Fig. 1c) the hydrology of Michigan streams is spatially quite variable. The hydrographic properties of a particular stream reflects the relative contributions of groundwater and runoff sources. For example, the Manistee River (Fig. 2a) drains large regions of highly conductive, relatively flat, outwash plain. More than 90% of its annual discharge is delivered by groundwater sources (Hendrickson & Doonan, 1972); flow variation is minimal, and water temperatures are cool (< 22 °C) during the summer allowing trout populations to flourish. The Jordan River (Fig. 2b) likewise receives a massive supply of groundwater throughout the year. However, because this catchment includes (besides outwash) large areas of morainal tills with higher slopes, it generates somewhat more runoff than the Manistee. Spring melt and storm flows are higher as can be seen in the left-hand portion of the Jordan's flow duration curve. The Au Gres River (Fig. 2c) is more similar to the majority of continental rivers (Poff & Ward, 1989; Allan, 1995). Runoff is the predominant source of water to the channel and summer temperatures are higher, usually exceeding the thermal tolerance limits of both brook and brown trout. In Michigan, fish communities in this type of stream are dominated by cyprinids, catostomids and centrarchids (Hendrickson & Doonan, 1972; Seelbach & Wiley, 1996; unpublished data).

The hydrological processes that generate groundwater and runoff flow are shaped by landscape characteristics in the catchment basin. The strength of this dependence is reflected in the fact that hydrologists and river managers for some time have routinely employed hydraulic geometry equations (Leopold & Maddock, 1953) expanded with land use/land cover and geological variables (Bent, 1971; Thomas & Benson, 1975; Holtschlag & Croskey, 1984; Osborne & Wiley, 1988) to predict hydrographic behaviour for catchments lacking stream gages. Inclusion of GIS technologies in the development of these predictive

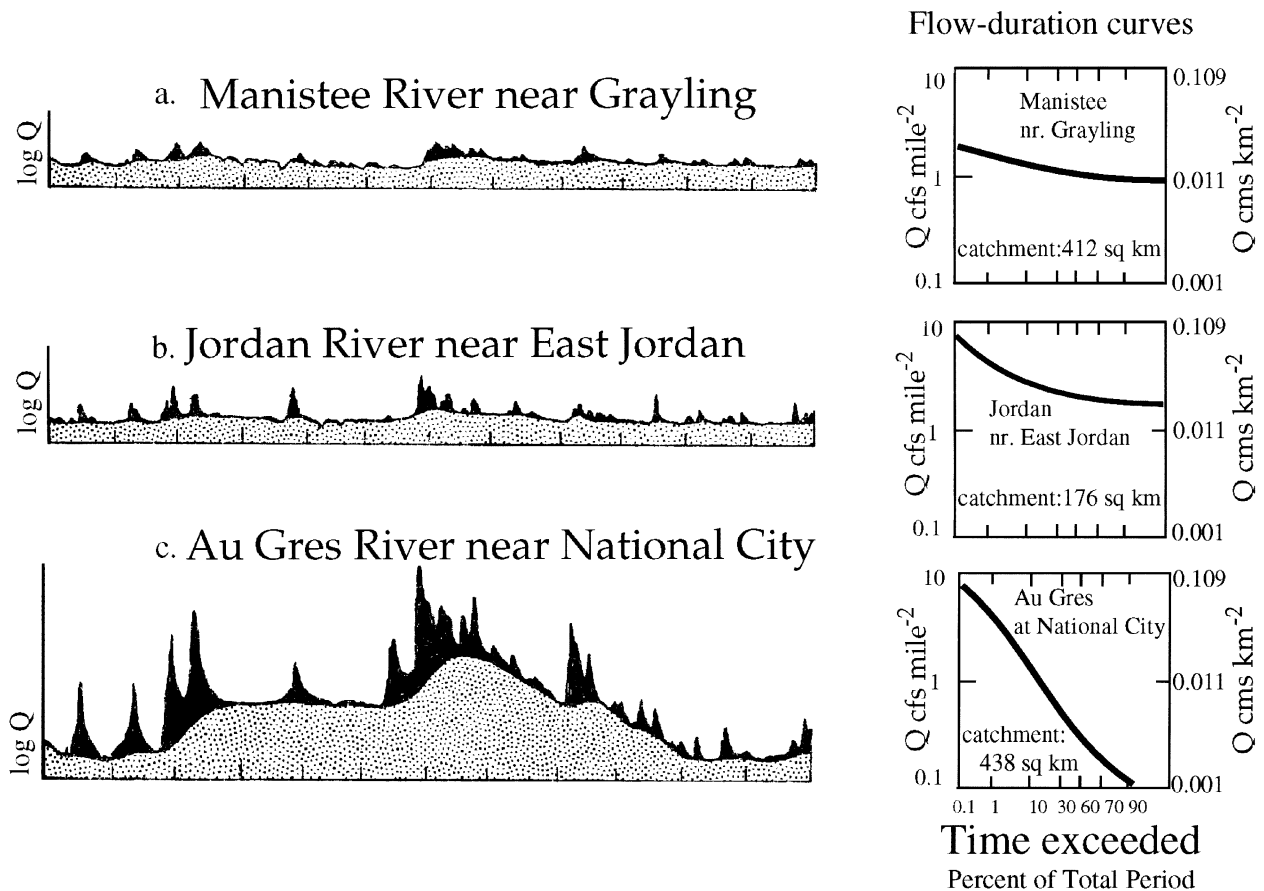


Fig. 2 (a–c) Example annual hydrographs and corresponding flow duration curves for three hydrologically distinct Michigan rivers. Shading in hydrographs separates baseflow and runoff components. Note that the Y-axis is logged for the hydrographs, and that both hydrographs and flow duration curves are standardized per unit catchment area. Redrawn from figures in Hendrickson & Doonan (1972).

equations is quickly becoming routine. For example, in conjunction with researchers at the Institute for Fisheries Research (Michigan Department of Natural Resources), we (Seelbach & Wiley, 1997) have developed (and presently employ in state agency management settings) synthetic flow duration curve models based on GIS analysis of mapped landscape characteristics (Fig. 1, Table 1) at USGS gaging sites. The inclusion of GIS-evaluated catchment characteristics in hydraulic geometry relations significantly improves the precision of estimating models, and allows Michigan fisheries scientists to predict with considerable accuracy the hydrographic character of ungaged river sites throughout the state.

Because the shape of the flow duration curve reflects the relative importance of groundwater sources for a site, it also provides information about temperature regime and associated biological communities. Even

without any information at the local site about habitat or channel characteristics, it is still possible to produce reasonably accurate models of trout population density using only landscape-scale variables (Table 2). In Michigan, where trout streams enjoy a higher level of legal protection than warm water streams, simply determining whether or not a site will support trout can have important regulatory implications. Landscape variables can be used to estimate the probability that a site will support trout and therefore warrant special environmental protections. Logistic regression (Retherford & Choe, 1993; Johnson & Gage, this volume) is particularly well suited for this type of landscape analysis and is being used in Michigan to develop a trout stream classification system applicable by a GIS-linked computer system to any site in the lower peninsula (Table 3).

From a landscape-scale perspective, then, these trout

Table 1 Relative fits (R^2 values) for Synthetic Flow Duration Curve Models of streamflow in Michigan's lower peninsula. The form of these MLR models is:

$$Q_{ex} = a * \text{Catchment area}^{b1} * \text{landscape_factor1}^{b2} * \text{landscape_factor2}^{b3} * \dots * \text{landscape_factorN}^{bN-1}$$

Landscape factor variables are derived from GIS analyses of statewide digital map covers and include: mean annual precipitation, average catchment slope, % urban landcover, % agricultural land cover, % forested land cover, % catchment in peaty soils, % catchment in lakes, ponds and non-forested wetlands, % catchment in glacial outwash

| Exceedance frequency (%) | R^2 for groundwater streams | R^2 for runoff streams |
|--------------------------|-------------------------------|--------------------------|
| 05 | 0.96 | 0.99 |
| 10 | 0.97 | 0.98 |
| 25 | 0.97 | 0.96 |
| 50 | 0.97 | 0.93 |
| 75 | 0.94 | 0.91 |
| 90 | 0.93 | 0.91 |
| 95 | 0.92 | 0.90 |

Q_{ex} is the daily average discharge in cms with an exceedance frequency ex , i.e. the discharge Q_{ex} is equalled or exceeded ex percentage of the time over a 10 + yr sample.

Table 2 Multiple regression analysis of ln total trout density (brook, brown and rainbow trout combined) predicted from landscape variables generated by GIS analyses. Data from 65 gaged sampling stations (Seelbach & Wiley, 1997)

ANOVA table

| Source | Sum of squares | d.f. | Mean square | F-ratio |
|------------|----------------|------|-------------|---------|
| Regression | 213.761 | 5 | 42.8 | 31.3** |
| Residual | 80.5707 | 59 | 1.36561 | |

| Variable | Coefficient | SE of coefficient | t -ratio |
|--------------------------------|-------------|-------------------|------------|
| Constant | 42.7904 | 16.41 | 2.61* |
| ln temperature (°C) | -8.13521 | 5.105 | -1.59* |
| ln lentic ¹ | -0.170835 | 0.0645 | -2.65* |
| ln SCS RCN ² | -2.87184 | 1.514 | -1.90* |
| ln coarse outwash ³ | 4.75151 | 1.392 | 3.41** |
| ln lanes index ⁴ | -1.94691 | 0.4367 | -4.46** |

¹Proportion of catchment in lakes, ponds and non-forested wetlands.

²Average (U.S.) Soil Conservation Service (SCS) average runoff curve number (RCN) for the catchment. The RCN is a key hydrological parameter in the SCS synthetic unit hydrograph model (SCS, 1986); it reflects soil and land use related contributions to the generation of surface runoff.

³Proportion of catchment with ice contact sand and gravel geology; based on GIS summaries of a digital version of the quaternary map of Farrand & Bell (1984).

⁴Standard deviation of the log_e of flow duration curve percentiles (Lane & Lei, 1950).

**Statistically significant at alpha < 0.01; *statistically significant at alpha < 0.05.

$R^2 = 0.726$ R^2 (adjusted) = 0.703.

SE of regression = 1.169 with 65-6 = 59 d.f..

stream communities appear to owe their existence primarily to the favourable alignment of a few large-scale hydrogeological factors. In this view, landscape composition appears to be the primary constraint shaping stream community structure, and landscape analysis is therefore an essential tool for stream ecologists.

At the same time, the view emerging from years of more traditional site-based studies in Michigan trout

streams is one of strong biotic interactions, and high endogenous (site-specific) annual variability. For example, local regimes of predation, competition and pathogens appear to influence strongly both algal and macroinvertebrate populations (Wiley, 1980; Wiley & Kohler, 1981; Hart, 1983, 1985, 1987, 1992; Kohler, 1984, 1992; Kohler & McPeck, 1989; Hart & Robinson, 1990; Kohler & Wiley, 1992; Creed, 1994). Recent work on epizootics in these streams demonstrates that major

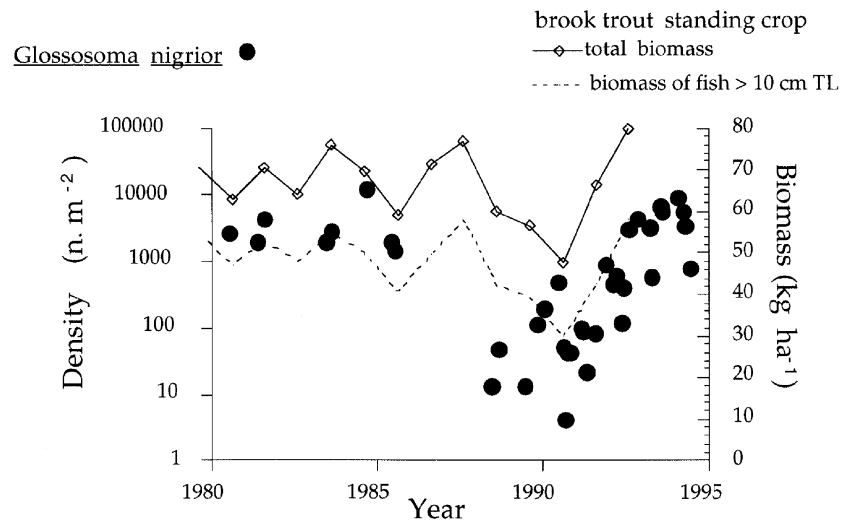


Fig. 3 Population time-series data from Hunt Creek illustrating a microsporidian-induced collapse of *Glossosoma nigrrior*, and covarying brook trout population.

Table 3 Logistic regression analysis of probability of finding trout (brook, brown or rainbow) at 56 gaged sites in Michigan's lower peninsula. Data from 65 gaged sampling stations (Michigan Rivers Inventory database; Seelbach & Wiley, 1997). Dependent variable was binary presence or absence data. Predictor variables as defined in Table 2. Predictive equation is of the form: Probability = $1/(1 + e^{-z})$; where $z = \alpha + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n$

| Variable | β | Exp(β) | SE | Wald statistic (d.f.) | Probability level [$\beta = 0$] |
|----------------|---------|----------------|---------|-----------------------|-----------------------------------|
| ln lanes index | -4.9136 | 0.0073 | 1.9245 | 6.5189(1) | 0.0170 |
| ln SCS RCN | -6.1862 | 0.0021 | 2.8830 | 4.6042(1) | 0.0319 |
| Constant | 22.6967 | | 12.1268 | 3.5029(1) | 0.0613 |

| Observed | Predicted Absent | Predicted Present | Percentage predicted correctly |
|----------|------------------|-------------------|--------------------------------|
| Absent | 49 | 2 | 96.08 |
| Present | 3 | 11 | 78.57 |
| Overall | 92.31 | | |

changes in food web composition and structure occur over 3–10-yr periods in many Michigan trout streams, driven by episodic outbreaks of microsporidian pathogens (Kohler & Wiley, 1992). For example, disease-induced collapses of *Glossosoma nigrrior*, a dominant herbivore in these systems, have had strong direct and indirect effects on the rest of the community. Algal populations increase, as do previously suppressed competitors which require the same algal food supply (Kohler & Wiley, 1997). Higher in the food web, brook trout populations also show some evidence of being indirectly affected by these pathogen outbreaks (Fig. 3).

Likewise for fish populations, local (site-specific) processes have been viewed for several decades as

primary factors regulating populations in Michigan trout streams (Ellis & Gowing, 1957; Shetter & Alexander, 1964; McFadden, Alexander & Shetter, 1967; Latta, 1969; Hildebrand, 1969; Laarman, 1969; Alexander, 1977a,b, 1979; Stauffer, 1979; Gowing & Alexander, 1980; Fausch & White, 1981, 1986; Alexander & Hansen, 1983; Fausch, 1984, 1988; Seelbach, 1987, 1993; Ziegler, 1988; Alexander & Nuhfer, 1993; Nuhfer, Clark & Alexander, 1994; Clark & Nuhfer, 1995). Large temporal variations in population sizes of brook and brown trout are routinely observed in longer data sets available from these streams (e.g. Figure 4). The most intensively studied Michigan trout populations (20 + yrs of data) vary in density by a factor of 3 to > 12 (Nuhfer & Alexander, 1993; Clark

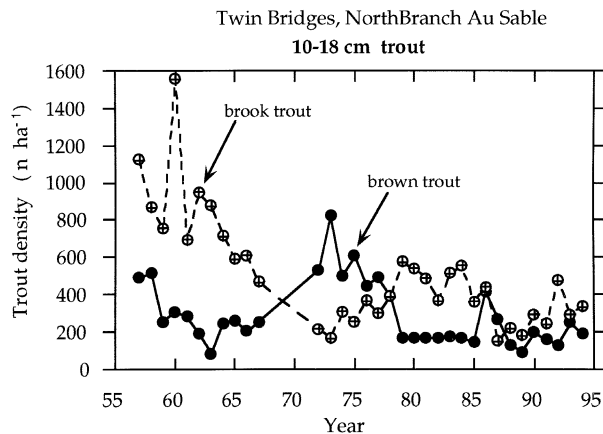


Fig. 4 Long-term variability in coexisting brook and brown trout populations. Data courtesy R. Clark and A. Nuffer, Institute for Fisheries Research, Michigan Department of Natural Resources.

& Nuffer, 1995); driven by a variety of site-specific mechanisms including annual variability in local habitat quality, climatic variation, competition and predation, habitat alteration and fishing pressure. Strong, endogenous community dynamics driven by site-specific (and often biologically controlled) processes, then, seem the rule when these trout stream communities are examined from a local (site-based) perspective.

Decomposition of variance: an analytical framework

Years of site-based analyses suggest that the biological communities of Michigan trout streams are highly variable over time, exhibiting site-specific dynamics often driven by endogenous community processes, such as predation, competition and disease. However, landscape analyses indicate that the same communities are relatively predictable assemblages shaped by the large-scale structure of the landscape. Which view is correct? Are these trout stream communities structured by relatively static hydrogeological patterns in the landscape? Or are they locally controlled and structured by internal dynamic processes? Our view reflects the scale of our analysis. Clearly, the correct answer is that Michigan trout streams are both physically and biotically structured. However, an appropriate analytical framework is necessary to engage a comprehensive analysis.

A useful analytical approach in which both perspectives can be integrated is to partition the total variance in the abundance of a particular species into site

location, time, and site-time interaction components using standard two-way ANOVA techniques (Lewis, 1978; Magnuson, Benson & Kratz, 1990; Matthews, 1990; Kratz *et al.*, 1995). The resultant partitioning of variances identifies three sources of variation which roughly correspond to three common ecological paradigms (Fig. 5).

Variance due to geographical locale (site treatment in an ANOVA) is spatial. It represents variation (time averaged) found between sites at different points in the landscape. Data required to estimate this variance must be spatially extensive; GIS and related map analysis techniques are the appropriate analytical tools, and landscape ecology (in the broad sense) is the corresponding ecological paradigm. Typical driving (causal) variables responsible for spatial variation include soils, geology, climate, land cover properties, and other readily mapped, large-scale variables.

Variance due to differences between years (year treatment in an ANOVA) represents annual variation averaged across locales. Annual variance in this context has been called 'coherent' time variation (Magnuson, Benson & Kratz, 1990; Kratz *et al.*, 1995) in that it represents variation in time that occurs simultaneously across all spatial units of the analysis. In the present study the term 'regional-time' is preferred to emphasize that this component of the variance represents regionally synchronous variation and therefore must have regional-scale causal mechanisms. Possible causal mechanisms might include climatic variation, anthropogenic alteration of the landscape or exploitation, large-scale epizootics, or invasions by exotic species. Analytical techniques lean heavily towards numerical simulations, linear modelling and time series analysis.

A third component of variation is given by the interaction term in a two-way (site \times time) ANOVA design. This term represents variation in time that is not synchronous across the set of site locations, i.e. site-specific variation in time. Kratz *et al.* (1995) refer to this as 'incoherent' temporal variance. It can be suggested that this 'site-specific-time' variation is essentially the focus of community ecologists as it includes the dynamics of the local community. Causal processes leading to incongruent variation at a site may be physical (e.g. point source effects) or biological (endogenous community dynamics arising from competition, predation or disease) but must be local (site-specific rather than regional) in effect, or at least locally

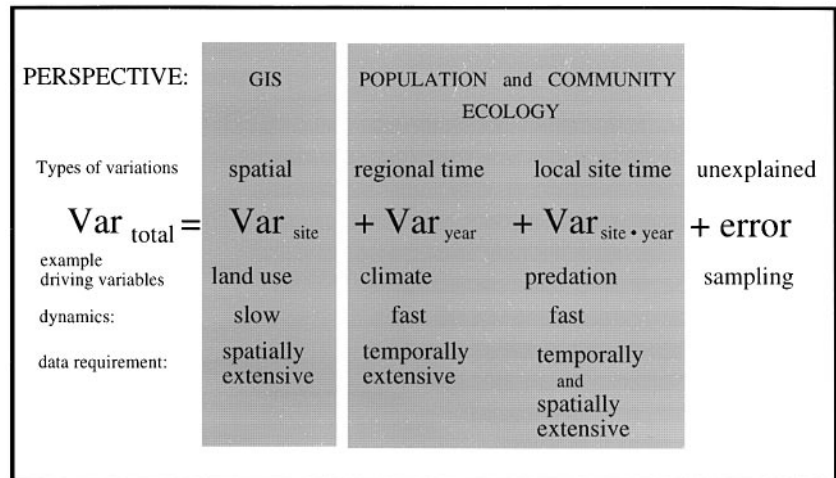


Fig. 5 Decomposition of variances by factorial ANOVA. Site treatment, year treatment, and their interaction term partition variation into three major categories which reflect distinct ecological scales and driving variables.

mediated in some distinctive fashion. Variables of interest include population characteristics, resource levels and local disturbance regimes. Analytical approaches often employed include simulation and differential equation models, linear programming models, and in contemporary community ecology there has been a distinct emphasis on *in situ* experimental manipulations (e.g. Hart & Robinson, 1990; Kohler, 1992).

A final component of variation is the error term, which includes any residual variance associated with measurement error or other unaccounted processes. The relative magnitudes of these four variance components can strongly influence both the structure and interpretation of spatially extensive data sets. The variance structure of a population is of more than statistical interest, because it implies something about the relative importance of various ecological processes operating at distinctive spatial and temporal scales. A decomposition of variances therefore can provide a useful framework for placing analyses with limited spatial or temporal extent into an appropriate larger-scale context.

Methods

Population variance structures in Michigan trout streams

To illustrate this approach population data were analysed for several invertebrate and fish species in the Michigan trout streams discussed above. The fish data come from long-term data sets developed by the Institute for Fisheries Research at four permanent

monitoring sites on the North Branch, Main Branch and South Branch of the Au Sable River (Fig. 6). Annual population estimates were based on the Bailey modification of the Petersen mark-and-recapture method (Bailey, 1951; Ricker, 1975) using 240 V direct current electrofishing gear. The 95% error bounds of the estimates were generally small (< 10% of the estimated population). Because mark-recapture estimates were used, sampling variance does not appear as a separate term in the ANOVA for fishes, but any effects attributable to it are included in the variation associated with interaction term (i.e. site-specific-time variance). Computationally, the site-time interaction term was estimated as the difference between the total variation and that variation explained by site and year effects ($SS_{\text{total}} - (SS_{\text{yr}} + SS_{\text{site}})$).

Invertebrate data were collected from five long-term study sites in the Thunder Bay, Cheboygan, Kalamazoo and several smaller Lake Michigan coastal basins as a part of an ongoing study of trout, food-web dynamics (Fig. 6, Kohler & Wiley, 1992, 1997). Quarterly or more frequently, insect population estimates were based on replicated ($n = 5-10$) rock cluster samples. Because samples were replicated on each date, residual (sampling) error was separately estimated by the ANOVA and is not included in the interaction term as was the case for the fish analyses.

In both the fish and insect analyses, variances were partitioned using standard factorial ANOVA techniques. Variation (sums of squared deviations) associated with each of the three components of interest ($SS_{\text{yr}}, SS_{\text{site}}, SS_{\text{yr} \cdot \text{site}}$) was expressed as a proportion of the sum of the three components ($SS_{\text{total}} - SS_{\text{error}}$ for the insects; SS_{total} for the fish). The proportional distri-

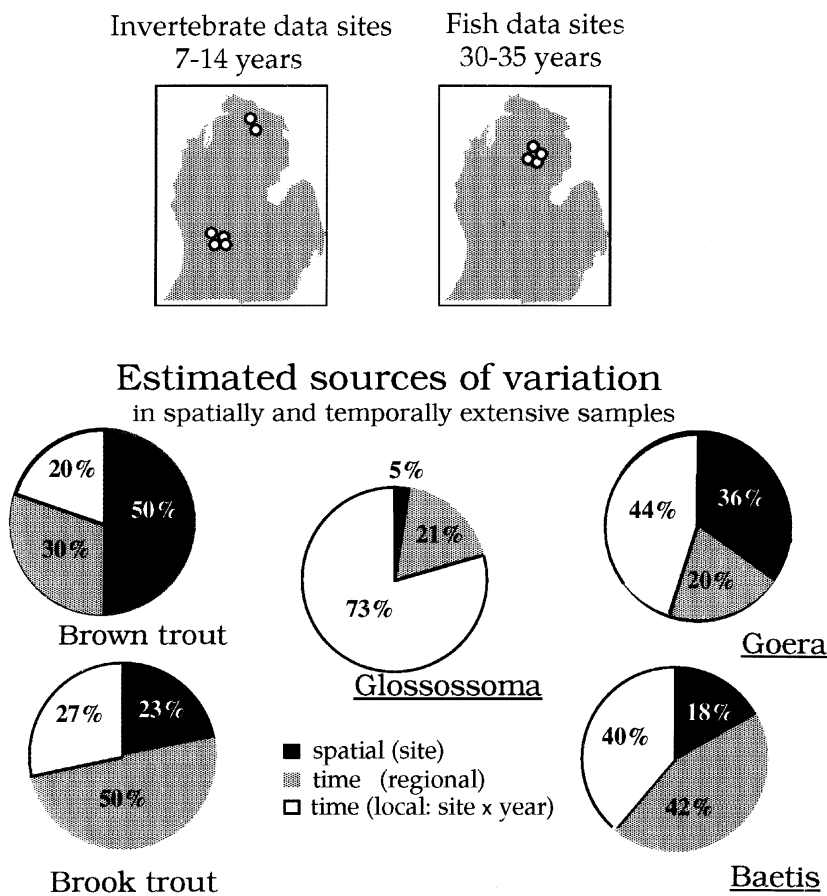


Fig. 6 Variance structure based on two-way ANOVAs for five common trout stream taxa. $n = 35$ yrs for trout; $n = 9$ yrs for aquatic insects. See Table 4. There was a unique variance signature for each taxon in the analysis which reflects the relative contribution of each of the variance components.

bution of this variation over the components of interest is referred to in the discussion below as the 'variance structure' of the data. It is of interest because, as argued above, each variance component can be associated with mechanisms operating at distinct temporal and spatial scales. As the ANOVA was used to partition sources of variance (i.e. to estimate the various sums of squares), a factorial design is required to generate the year-site interaction term. We are not in this context testing hypotheses about the statistical significance of treatment factors. Nested designs (e.g. repeated measures) may be used to test hypothesis about site differences in similar data sets, but cannot be used in this context because they assume interaction effects are zero.

Results

The variance composition for each taxon examined was distinctive, although several interesting patterns emerged (Fig. 6, Table 4). The two trout species were similar in that site-specific dynamics constituted 25%

or less of the total variance whereas among the insects examined site-specific temporal variation was substantially larger. *Glossosoma nigrior* and *Goera stylata* were the most influenced by site-specific-time variation. This is consistent with the known ecology of both of these species, as *Glossosoma* is strongly regulated by microsporidian parasites (see above) and *Goera stylata* is strongly suppressed by periodic competition with *Glossosoma* (Kohler & Wiley, 1997). Regional-time variation (coherent variance) was particularly high for both brook trout and *Baetis* spp. This suggests that these taxa may be strongly influenced by region-wide climatic or hydrological variation, possibly mediated proximally by changes in groundwater loading. Spatial variance (site location) was most important to brown trout and *Goera stylata*. These two taxa appear to have more specific habitat requirements in the sense that site-specific features strongly and consistently influence population size.

ANOVAs were also performed for a series of subsamples with arbitrary start dates, and of serially increasing sample length, in order to examine how

Table 4 Design summaries from factorial ANOVA's of representative taxa from Michigan trout stream communities. d.f. = degrees of freedom. ANOVA results in Fig. 6

| Taxa | Total observations (total d.f.) | No. of sites (d.f.) | No. of yrs (d.f.) | Sample dates per yr per site (d.f. sampling error) |
|---|------------------------------------|------------------------|----------------------|---|
| <i>Glossosoma nigrior</i> (Trichoptera: Glossosomatidae) | 114 (112) | 5 (4) | 9 (8) | 2–6 (68) |
| <i>Goera stylata</i> (Trichoptera: Goeridae) | 108 (106) | 5 (4) | 9 (8) | 2–6 (62) |
| <i>Baetis</i> spp. (Ephemeroptera: Baetidae) | 89 (87) | 5 (4) | 9 (8) | 2–6 (43) |
| <i>Salvelinus fontinalis</i> (brook trout) | 124 (122) | 4 (3) | 35 (34) | 1 (no estimate) |
| <i>Salmo trutta</i> (brown trout) | 124 (122) | 4 (3) | 35 (34) | 1 (no estimate) |

the estimated variance structure of the individual taxa changed with increasing temporal extent of sampling (Fig. 7). Again the result for each taxa was distinctive, but, in all cases the estimated variance structure was highly dependent on the length of the period sampled. Trout species required a sample of 10 (brook trout) to 20 (brown trout) yrs duration to stabilize the variance estimates. Insect variances required approximately 5 yrs of data to stabilize.

In samples of short duration the contribution of spatial variance was always strongly overestimated (see Fig. 7). Conceptually, this can be thought of as being due to a failure to estimate reasonably the true mean value for the time treatment and its interaction with spatial variance. A substantial sample of the time series is needed to stabilize estimates of the temporal mean and variance, and therefore to partition correctly the observed variance between space and time components. An extreme example of this spatial bias will occur when a spatially extensive sample is taken with no replication over time. All variance will necessarily appear to be spatial (i.e. variance between sites), even if spatial constraints really account for only a small portion of the true variation (as in the case of *Glossosoma nigrior*).

Discussion

Implications for study design and interpretation

Long-term data sets from a number of Michigan trout streams were used to examine the sources of variation in abundance of several key invertebrate and fish

species. From this analysis emerge several important, practical issues related to the problem of evaluating the relative roles of local and landscape mechanisms in shaping observed communities:

1 Variance structure is a species-specific property. Each taxon examined had a distinctive overall variance structure when the whole data series was analysed. Furthermore, in every species, variance structure (i.e. the apparent proportional contributions of the variance components) varied with sample size in a unique and characteristic fashion. Similar results have been reported whenever the individual members of a community have been examined (riffle fishes: Matthews, 1990; zooplankton: Kratz, Frost & Magnuson, 1987). It can be argued that the observed variance structure reflects the relative contributions of ecological mechanisms operating on that population at distinctive spatial and temporal scales and therefore contains useful information about the ecology of the taxon. For example, *Glossosoma nigrior* populations are frequently regulated by local pathogens (in this case *Cougourdella*: Sporozoa). Its variance structure reflects this fact, indicating that endogenous components predominate and spatial variance within this set of sites is relatively unimportant. Further, differences between the variance structures of brook and brown trout from the same set of locations, suggest inherent ecological differences which might have useful management implications.

The species-specific nature of variance structures is noteworthy also because it implies that no characteristic variance structure exists for the trout stream community as a whole. As key trout stream species appear to respond independently to ecological

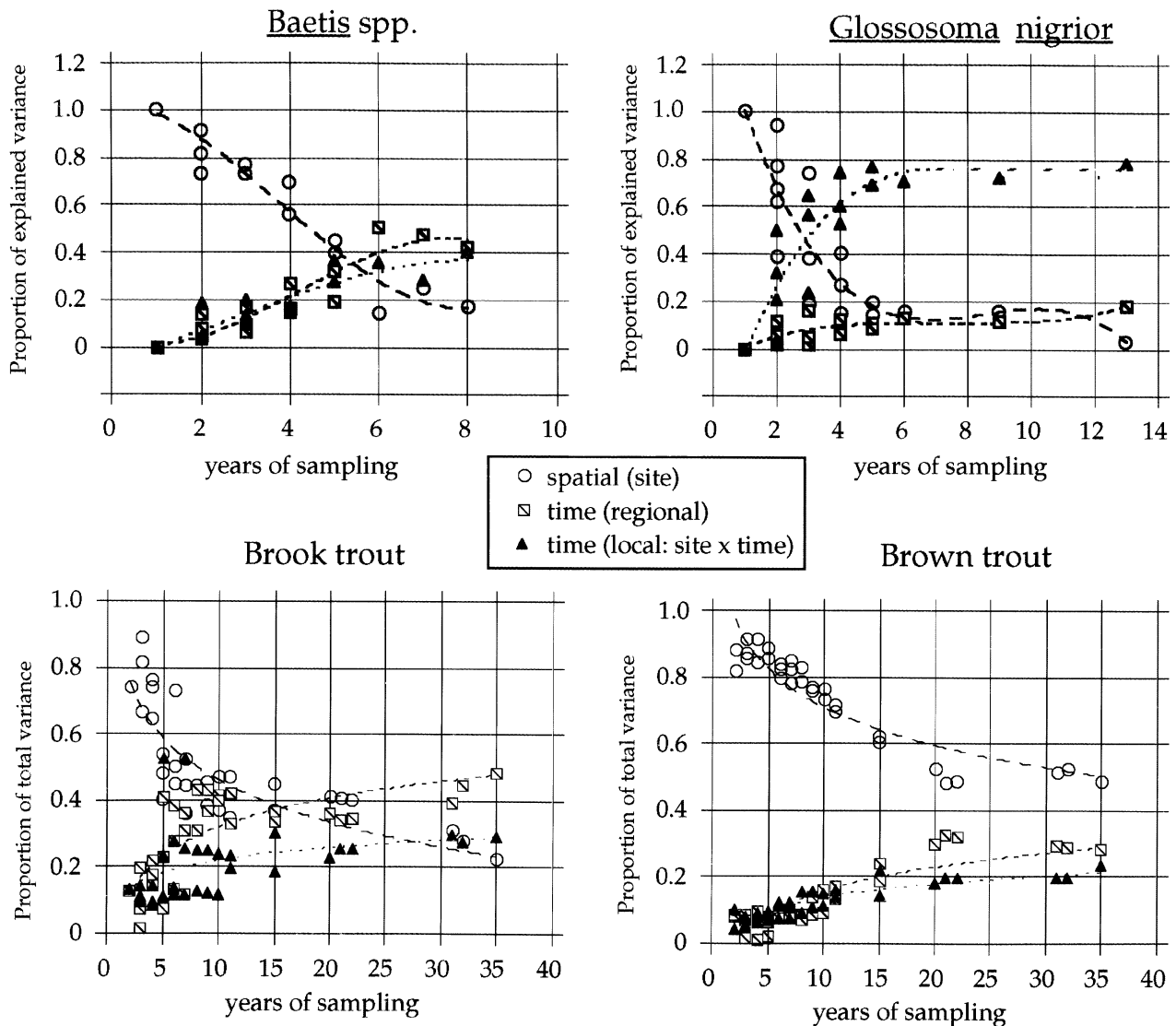


Fig. 7 Variance structure estimated by ANOVA changes with the length of time the population is sampled until the sample is large enough to stabilize estimates of the temporal and spatial means.

processes occurring at different scales of time and space, human-induced stresses on the landscape ecosystem can affect members of this local community differentially. This is consistent with the observation that community composition in streams is often more sensitive to environmental change than are functional or community-level variables (Karr, 1991).

2 Estimates of spatial variance can be inflated by undersampling in time and this may lead to erroneous attribution of explanatory power to landscape (spatial) mechanisms. Over-fitting of models to account for what falsely appears to be spatial variation is a real danger in this respect. For example, the analysis of

single-season (or year) survey data sets, using GIS techniques is not uncommon because of the high costs of gathering spatially extensive data. Variance in dependent variables of interest, however, which might be statistically explained by landscape character data from a GIS, may be erroneously estimated and attributed to site location or site attributes. High R^2 values for a regression cannot guarantee that spatial variance is correctly identified (hence the oft-repeated warning that correlation-based models imply association and not causation). Monte Carlo re-sampling of the brown trout data illustrates this problem nicely (Fig. 8). The variance estimates achieved with < 10 yrs

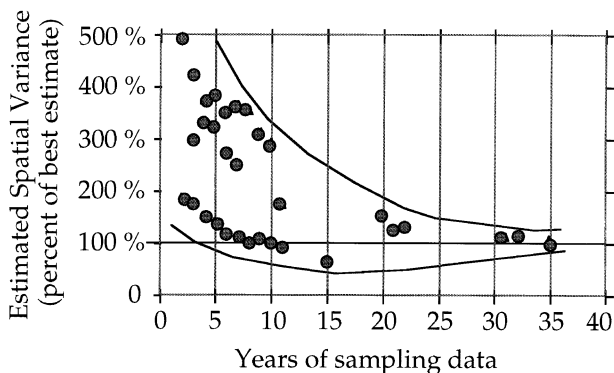


Fig. 8 Apparent spatial variation in a series of subsamples of varying length with arbitrarily chosen starting dates. Data are for brown trout at four sites in the Au Sable River system. Note that data sets less than 10 yrs in length give poor predictions of the long-term (20 + yrs) average values.

of sampling may or may not accurately estimate the true extent of spatial variation in the field.

Requiring the explicit identification of ecologically reasonable mechanisms in model construction provides some safeguard against erroneously attributing temporal variance to spatial variables. But ultimately, the only sure defence against erroneous estimates of spatial variance is an adequate long-term temporal sample. In the present analyses fish populations required at least 15–20 yrs (roughly ten or more generations) of data to stabilize estimates of the variance structure. Insects generally required a shorter sample of 5–7 yrs, but as they have faster and shorter life cycles, this still amounts to ten or more generations for a bi-voltine *Glossosoma* and *Baetis*.

3 Variance structure affects the analytical relevance of landscape variables. Taxa for which time (regional and site-specific) variance components are small, should be more easily predicted from landscape variables than those with high endogenous or regional temporal variances. As the variance structure of individual species can be quite different, we might expect to find substantial variation in the explanatory power of spatial analyses when applied to members of the same community.

This study attempted to examine this premise by modelling brook and brown trout population densities in Michigan's lower peninsula from mapped landscape variables using a large independent data set and GIS (Seelbach and Wiley, 1996). Brown trout had a stronger spatial variance component than did brook trout in the analysis above (Table 5). Conversely, site-specific time variance was larger for brook trout than for

brown trout in the same set of streams suggesting community interactions may be more important to their population dynamics. The best-fit regression model for brown trout (based on mappable landscape variables) explained 65% of the total variation in their density across fifty gaged sampling sites. This is roughly consistent with the spatial variance estimate from the long-term data sets discussed earlier in this paper, which indicated that about half the total variance was spatial (Fig. 6).

Regression modelling of brook trout proved more difficult. Using only landscape variables, the best-fit model had an R^2 of 0.302 (Table 5). This, however, is consistent with this species' estimated spatial variance component in the previous analysis of only 23% (Table 9). Competition with brown trout is a widely recognized influence on the population dynamics of brook trout (see above). When appropriate terms for brown trout were included in the regression model the fit improved substantially ($R^2 = 57%$). In this case a quadratic term is appropriate because in an extensive spatial sample both species are restricted to the same set of cold water streams (and therefore positively correlated at low densities), but brown trout tend to suppress brook trout at high densities, which leads to the negative term in the quadratic. The proportion of the total variance related to effects of brown trout alone was small (13%) as was the site-specific-time component (endogenous variance) in the earlier analysis (27%, Table 4). The remaining unexplained variance roughly equals the remaining regional-time component (43% and 50%, respectively). Thus, it appears that differences in ability to predict population size from the landscape level are generally consistent with observed differences in the estimated variance structure of the two trout species.

4 Variance structure affects ability to generalize directly from site-specific results to large-scale pattern. Community ecologists strive to elucidate the underlying mechanisms driving population interactions and community dynamics. Field experiments at arbitrarily chosen study sites are commonly employed to help evaluate the roles of endogenous mechanisms, such as competition and predation (Schoener, 1983; Connell, 1983). Unfortunately, generalizations from the results of studies at specific sites are problematic when spatial variance is high (Wiens *et al.*, 1986; Pimm, 1991; Levin, 1992). Hypothesis testing about community processes in spatially extensive data sets can be problematic for

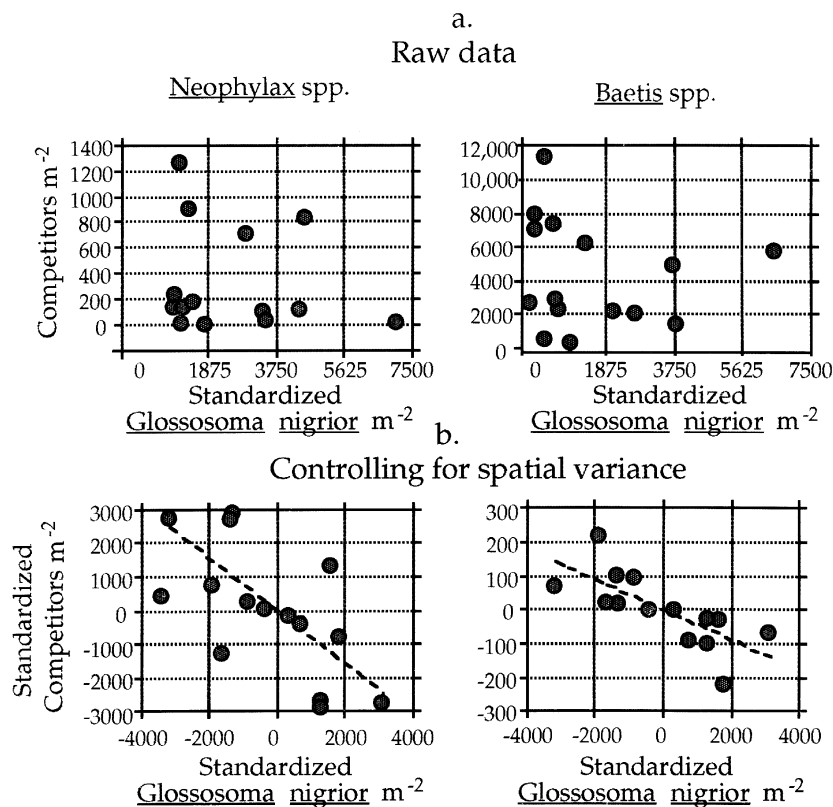


Fig. 9 Spatial variation can obscure patterns in community dynamics in spatially extensive data sets. (a) Raw data plots of *Glossosoma v* the density of two important groups of competitors (*Baetis* and *Neophylax*) showing no apparent relationship. (b) Plots of the same variables, with data standardized to site means in order to control for inter-site differences. Note the negative effects of *Glossosoma* on both taxa.

Table 5 Comparison of relationship between landscape variables and variance structure for Michigan brook trout and brown trout populations. Landscape variables used in multiple linear regression (MLR) models included: catchment size, groundwater index values, land use and hydrological parameters. Biological variable (brook trout model only) was brown trout density (a well documented competitor and predator of brook trout). Analysis based on unpublished data (R. Clark, P. Seelbach, M. Wiley and T. Zorn, Michigan Rivers Inventory: Institute for Fisheries Research [MNDR] and University of Michigan)

| Taxa | % sources of variation estimated by decomposition analysis ¹ | | | R^2 (as percentage) from Multiple Linear Regression models ($n = 50$) with: | | |
|-------------|---|---------------------------|---|---|--------------------------|------------------------|
| | Spatial (site effect) | Regional time (yr effect) | Local time (site \times yr) interaction | Landscape variables only | Biological variable only | Landscape + biological |
| Brown trout | 50 | 30 | 20 | 65.3 | – | – |
| Brook trout | 23 | 50 | 27 | 30.2 | 12.5 | 56.92 |

¹See Table 4.

²Compare with sum of spatial and site dynamics variance for brook trout.

the same reasons, unless inherent spatial variability can be evaluated. For example, detecting effects of competition between *Glossosoma nigrior* and other grazing insects in spatially extensive survey data is difficult even when a priori the effect is known to occur.

When data from seven different streams for which extensive time-series data are analysed together, there is little apparent correlation between *Glossosoma* and potential competitors (Fig. 9). This is despite the fact

that from site by site analyses that microsporidian collapses were followed by statistically significant increases in these taxa at every one of the included sites (Kohler & Wiley, 1997). Concluding that competitive effects were not significant based on such an analysis (i.e. no significant correlation in Figs 9a and 9b) would be quite erroneous. In this case, the inter-site spatial variance is large enough to obscure temporal variance attributable to *Glossosoma*. If the densities for the

competitors are normalized to their long-term site means, however, the effect of *Glossosoma* can be seen. Normalization by some statistical means (e.g. standardizing Z transformation, use of paired t -tests, or two-way ANOVA with a spatial treatment) focuses the analysis on the appropriate component of the observed variance (in this case site-specific-time). Understanding the variance structure of the populations studied is critical to a correct interpretation of spatially extensive data.

ANOVA as a conceptual framework

ANOVA-based decomposition of variances has provided a useful conceptual framework for integrating spatial and temporal data in Michigan trout streams and elsewhere (Lewis, 1978; Magnuson *et al.*, 1990; Matthews, 1990; Kratz *et al.*, 1995). An examination of variance structure in several representative taxa illustrates potential biases associated with both spatially extensive but temporally narrow (typical GIS) study designs, and with temporally extensive but spatially narrow (typical community ecology) study designs. For those interested in studying biotic mechanisms, substantial spatial (inter-site) variance limits the ability to generalize from results obtained at specific sites. When data are available from multiple sites, analysis should therefore include some control for spatial variation (e.g. paired t -test, site treatment in ANOVA, standardization to means, etc.). In GIS-based analyses it is important to remember that temporal variances can erroneously appear as spatial variation. Overfitting of models (i.e. entering a large number of independent variables to maximize the R^2 value) to these kind of data will almost certainly lead to an incorrect representation of ecological mechanism.

The ANOVA approach employed does not, however, neatly categorize all ecologically relevant sources of variation. For instance, source-sink dynamics do not easily fit into the ANOVA paradigm. Confluence effects on fish diversity in rivers contribute to spatial variance (time-averaged, between site variability). However, their local effect is the result of interactions with larger regional-scale processes, in this case the species pool available from the confluent branch (see Osborne & Wiley, 1992; Osborne *et al.*, 1992). The two-way ANOVA design employed in the present study also oversimplifies the hierarchical nature of spatial units in order to achieve a single interaction term

between time and space effects. It is easy to imagine a more realistic but complicated design in which spatial scale is represented by more than one treatment (e.g. site and major basin within a larger region). Such an analytical design would require two time-by-space interaction terms (one for each level in the spatial hierarchy) raising the possibility of higher-order interactions and requiring a much messier analysis and substantially larger data sets. Ecologists are just beginning to explore how to develop appropriate models to handle spatially and temporally complex data sets.

The large data requirement for a successful decomposition of variances into time and space components can also be a major obstacle to using this approach. Scale is an unavoidable issue when sampling in either space or time. Population variance structures observed in Michigan trout streams suggest that the apparent magnitude of temporal and spatial variance depends upon the length (time scale) of the sample series examined. While the issue was not examined here, it seems reasonable to expect that the spatial extent of the sample should also influence the observed variance structure. The observed variance structure may always have some dependence on the spatial and temporal extent of the sample. On the other hand, it is interesting to note that spatial variance tended to be more important for the trout than for the insects examined. This is despite the fact that the fish data set was from a much smaller geographical region compared with the insect data set. In extreme cases, outcomes are obvious. A spatially extensive sample taken on a single date will represent all inter-sample variance as being spatial (i.e. reflecting time-independent inter-site differences). Conversely, a long time series from a single site will necessarily represent all variation as being temporal and site specific.

Data series of ten or more generations seem to be required to estimate accurately means and variances in spatially structured data from Michigan trout streams.

Conclusions

For the last several decades ecologists have relied heavily on experimental approaches to isolate and identify specific ecological mechanisms. However, at the landscape level it is clear that important ecological processes involve physical and temporal scales which preclude direct experimental manipulation. GIS technologies are opening the door to spatially extensive

community analysis. A critical step in the integration of this tool with the rich but traditionally local perspectives of aquatic community ecology is a carefully balanced assessment of the biases and the strengths of both landscape and site-based analyses. Only in this larger context can a comprehensive view of local and regional mechanisms be forged.

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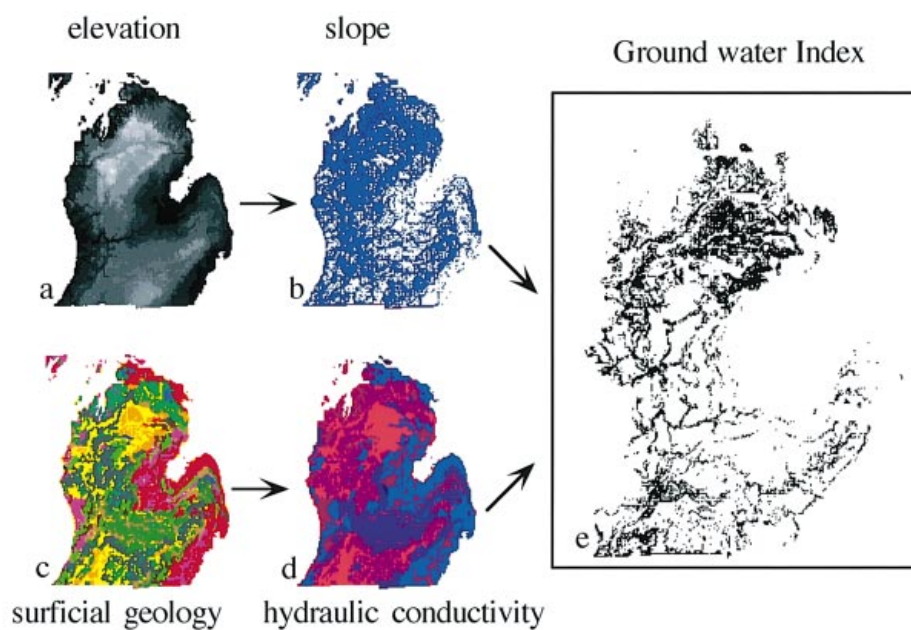


Fig. 1 Example GIS analysis of potential for groundwater loading to stream channels in Michigan's lower peninsula. Estimates based on raster modelling of Darcy's law: groundwater velocity = hydraulic conductivity (m day^{-1}) \times hydraulic slope. (a) Digital elevation map (USGS; resampled at 1 km^2 resolution) used to derive topographic slope map (b) Topographic slope map (m/m), (c) Quaternary Geology map (Farrand & Bell, 1982) used to derive (d) hydraulic conductivity map (m day^{-1}) (e) Michigan Rivers Inventory (Seelbach & Wiley, 1997) Ground Water Index (GWI). This index approximates groundwater flow velocity (m day^{-1}) for each square kilometre raster. Rasters with high values are expected to have high rates of groundwater to supply to surface streams, wetlands and lakes. The index was produced by multiplying map (b) raster values by map (d) raster values. The GWI values are being used in several classification and modelling projects by fisheries ecologists in the Michigan Department of Natural Resources.