Flood Disturbance and the Distribution of Riparian Species Diversity

Jacob Bendix

FLOOD DISTURBANCE AND THE DISTRIBUTION OF RIPARIAN SPECIES DIVERSITY*

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ABSTRACT. Biodiversity varies considerably in Southern Californian riparian vegetation. The intermediate disturbance hypothesis posits greatest diversity in settings that are subject to moderate-intensity disturbance. Flood intensity tends to vary systematically in watersheds, potentially imposing patterns of biodiversity. In two study watersheds, species richness increases with flood severity. Diversity, or heterogeneity, is less predictable: Biodiversity patterns in these watersheds are complicated by atypical patterns of flood severity. Although riparian diversity may be intimately dependent on flood disturbance, the relationship is predictable only with due attention to the physiographic details of individual stream networks. *Keywords: biodiversity, floods, riparian vegetation, stream power.*

$\mathcal{I}$n recent years, concern has increased for biodiversity and for land-management policies and techniques that favor the preservation of species diversity (Ehrlich and Wilson 1991; Franklin 1993; Nilsson, Jansson, and Zinko 1997). Riparian environments are important to biodiversity at two scales: Their presence contributes to regional biodiversity, and they are notable for their internal diversity as well (Malanson 1993; Naiman, Décamps, and Pollock 1993). The potential influence of hydrologic disturbance on the spatial distribution of riparian species diversity is presented in an empirical example from the Transverse Ranges of Southern California.

Theories concerning the spatial occurrence of plant species diversity often emphasize the role of disturbance regimes (Grubb, 1977; Petraitis, Latham, and Niesenbaum 1989; Malanson and Butler 1990; Hobbs and Huenneke 1992). If disturbance does affect diversity, it ought to be evident in riparian environments because they are particularly vulnerable to disturbance. Most—by some definitions, all—riparian zones witness periodic flooding, and floods are agents of disturbance.

The most prominent theory relating disturbance to species diversity is the intermediate disturbance hypothesis, which predicts maximum diversity in environments that experience moderate disturbance (Loucks 1970; Connell 1978; Petraitis, Latham, and Niesenbaum 1989). *Moderate* may refer either to disturbance magnitude or to disturbance frequency; this discussion concentrates on magnitude, or severity. According to this theory, intermediate-magnitude disturbance removes only a subset of the preexisting vegetation, thus making only a portion of the affected area available for colonization. Diversity is enhanced by the combination of disturbance survivors and the newly arrived disturbance exploiters (Figure 1). Partial alteration of sites by intermediate-magnitude disturbances may also create new microhabitats that in turn are occupied by diverse species (Hughes 1990; Savage, Reid, and Veblen

FLOOD MAGNITUDES   POST-FLOOD VEGETATION
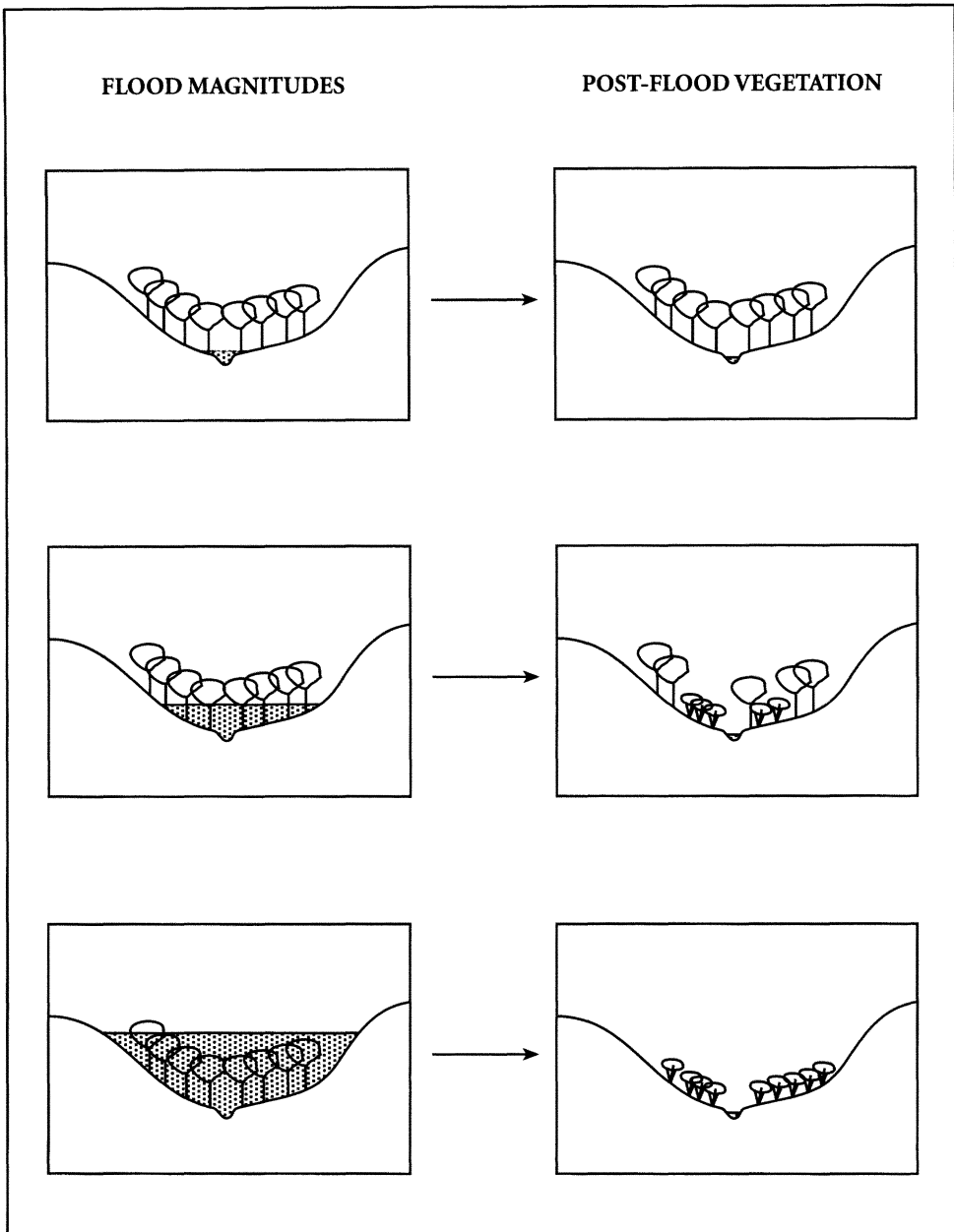
FIG. 1—A simple example of the intermediate disturbance hypothesis, with floods as the distur-
bance agent. A small flood (top) does little to damage the preexisting vegetation and thus has little
impact. An intermediate-magnitude flood (middle) fosters high diversity, because it removes
enough of the preexisting vegetation for the addition of pioneer species. An extremely large flood re-
sults in low diversity, because none of the preexisting vegetation remains to mingle with the pioneer
species.

1992). *Magnitude* may refer to either the areal extent of disturbance or its severity (Malanson 1984); in a fluvial setting, area and severity are likely to covary, for both the area inundated and the energy of flow increase as discharge increases (Dunne and Leopold 1978).

In riparian settings, flooding is a significant form of disturbance. A flood's destructive impact may be felt in several ways: through the imposition of anaerobic conditions by inundation; through the mechanical breakage of plants by floodwaters and/or the sediment they carry; or through erosion of the substrate in which the plants are rooted (Hupp 1988; Malanson 1993; Bendix in press). These impacts make floods a major element of disturbance in most riparian environments and the dominant one in many (White 1979; Bendix 1994a; Décamps and Tabacchi 1994). Apart from the direct impact on vegetation, alteration of site conditions is particularly significant at flood-affected sites where colonization by new species is further facilitated by the deposition of fresh alluvial substrate.

Because of the demonstrable importance of flood disturbance, studies that test the applicability of the intermediate disturbance hypothesis to riparian vegetation emphasize the distribution of flood magnitude, either as part of a presumed systematic downstream gradient of disturbance (Nilsson and others 1988, 1989) or as a variable across multiple watersheds (Baker 1990b). Results to date have been ambiguous, and complicated by differences in scale and methodology. The possible impacts of flooding on species diversity remain intriguing, because floods may impose a distinct spatial pattern on the distribution of species diversity.

DISTRIBUTION OF FLOOD IMPACTS

The systematic variation of hydrologic variables within watersheds has been quantified in a number of studies, beginning with early research on hydraulic geometry (summarized in Leopold, Wolman, and Miller 1964). The net result of these hydrologic patterns is that severity of flooding often varies systematically as one moves downstream through a watershed. The most basic pattern is:

$$Q \propto A \tag{1}$$

where Q is discharge (volume of water per time) and A is drainage area. Because drainage area increases downstream, discharge in most streams also increases with distance downstream. This common trend suggests that the disruptive force of floods should also increase as they move down through a watershed. But the actual impact of floods depends not so much on the amount of water as on the energy exerted by it, which is only partly determined by discharge.

Unit stream power, the actual energy per unit area exerted against the valley floor, has proved useful in determining both the geomorphic and ecological impacts of floods (Baker and Costa 1987; Bendix 1994a). It is determined by the equation

$$\omega = \gamma D S v \tag{2}$$

where ω is unit stream power in watts per square meter, γ is the specific weight of the water-sediment mixture in newtons per cubic meter, D is the average depth of flow in

meters, S is slope (dimensionless), and v is velocity in meters per second. Because γ is unlikely to vary significantly along a stream course, this equation indicates that unit stream power will change in a downstream direction as a function of the downstream variation of depth, slope, and velocity.

Downstream change in these variables is fundamental to hydraulic geometry, which refers to the geometric rate of change of hydraulic variables as discharge (Q) increases. These variables can be represented by the following equations (Leopold and Maddock 1953; Leopold and Miller 1956):

$$D = cQ^f \tag{3}$$

$$S = tQ^z \tag{4}$$

$$v = kQ^m \tag{5}$$

Coefficients c, t, and k and exponents f, z, and m can be determined empirically for any given stream. When applied to discharge figures for a given recurrence interval discharge, equations 3–5 describe how the hydraulic parameters react to the downstream changes in discharge. The regular, geometric changes in these variables suggest that there may be systematic patterns in the impacts of a given flood as it moves through a watershed (given equation 1, we should be able to substitute A for Q in these equations).

William Graf provided an example of such a pattern in the Henry Mountains of Utah, modeling changing values of stream power (Graf 1983). Such patterns are complex, for they may depend on a relationship between valley morphology and the magnitude of the flood in question (Magilligan 1992); and they may even change with erosional modifications of the valley bottom (Graf 1983). It should be noted that the downstream change will not necessarily involve an increase in stream power. Luna Leopold, M. Gordon Wolman, and John Miller reported average values of .30, –.95, and .20 for f, z, and m, respectively, for ephemeral streams in the western United States (1964). The negative value for z suggests that decreasing slope may offset the increases in depth and velocity as the flood moves downstream. In fact, Graf found that within a given watershed the pattern of stream power fluctuated between positive and negative downstream trends with historical changes in stream morphology (1983).

IMPLICATIONS FOR BIOTIC DIVERSITY

For all their potential complexity, the patterns of flood severity suggest that, if riparian species diversity varies with flooding, it should also vary systematically through the watershed. If we assume a gradient from minimal disturbance—due to small discharges—at a stream's headwaters to maximum disturbance at its mouth—the highest discharges—then the intermediate magnitude of disturbance, and hence the highest diversity values, should be found in the middle reaches of the stream (Figure 2a). Christer Nilsson and his coauthors addressed this possibility, with equivocal results. In studies of Swedish rivers, species richness was measured at regularly spaced reaches and regressed on distance downstream. No relationship appeared in their
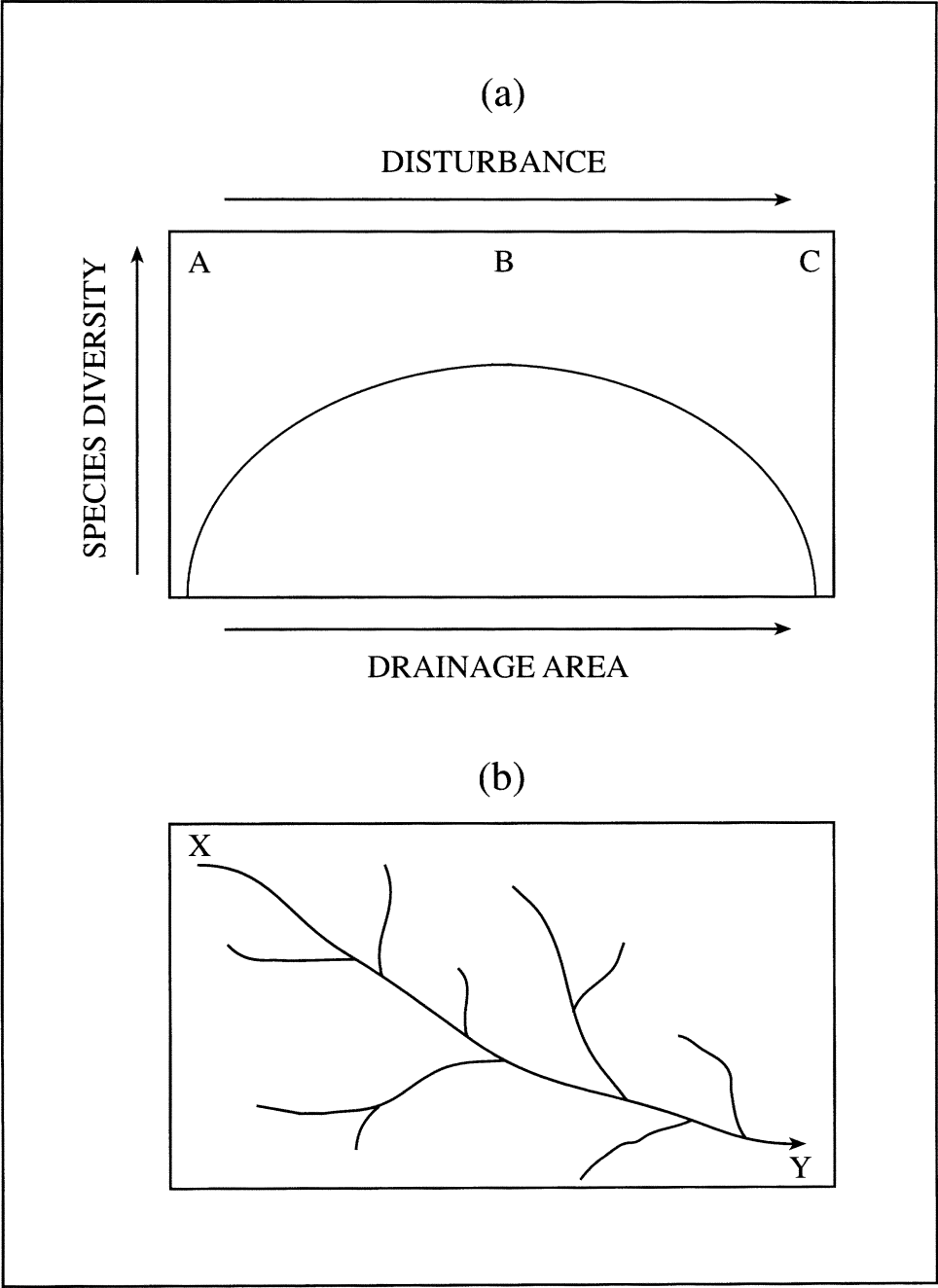
FIG. 2—Application of the intermediate disturbance hypothesis to a watershed setting. See the text for references to (a) and (b).

overall data, but when they limited their analysis to native species, richness peaked in the middle reaches (Nilsson and others 1988, 1989). It remains unclear whether this reflects an intermediate level of disturbance. The relationship was not matched by fluvial variables that indicate flood severity, and a decreased richness of natural species in lower reaches may have been caused by more human presence there, favoring weedy species.

Although it is tempting to assume that the intermediate disturbance hypothesis locates maximum diversity in a stream's middle reaches (Vannote and others 1980), actual patterns observed depend largely on the scale and location of the stream segments studied (Meentemeyer 1989; Bendix 1994b). For the intermediate disturbance hypothesis, *intermediate* refers to potential ecological impacts, not to potential flood magnitudes: A→C in Figure 2a may not coincide with X→Y in Figure 2b. In some small streams, for example, even the largest floods are insufficient to generate more than intermediate disturbance of the vegetation (there, X→Y would coincide with A→B). For such a stream, the location of *ecological* intermediate disturbance—and maximum diversity—may be expected downstream. In streams where even the uppermost reaches experience floods severe enough to create an intermediate disturbance, X→Y will coincide with B→C, with diversity decreasing downstream. Thus if the intermediate disturbance hypothesis does hold true in fluvial settings, it may result in either a near-linear (positive or negative reflecting A→B or B→C) or a quadratic relationship (A→C) between species diversity and location within the watershed, all depending on the relationship between flood magnitudes and ecological sensitivity.

Figure 2 remains based on an assumption that discharge—which varies most reliably with drainage area and watershed position—equates to potential disturbance. Disturbance is, however, actually quite dependent on variation in the hydraulic components of stream power. Any prediction of where intermediate disturbance and maximum diversity would be found in a watershed has to be mediated by understanding its hydraulic geometry and the resulting distribution of stream power.

Apart from studies by Nilsson and his associates, the ties between hydrologic trends and patterns of riparian biodiversity have received little attention. Studies have related riparian diversity to positions within the drainage network, including Cliff Hupp in Virginia (1982), Eric Tabacchi, Anne-Marie Planty-Tabacchi, and Odile Décamps in France (1990), and R. Carbiener and A. Schnitzler in the valley of the Rhine (1990). Each placed greater emphasis on geologic controls in fluvial morphology than on overall patterns in a drainage network. William Baker did examine riparian species richness in Colorado in relation to the intermediate disturbance hypothesis, but on a regional, rather than watershed, scale (Baker 1990b).

As the foregoing discussion indicates, our understanding of patterns in riparian diversity may be substantially enhanced by drawing on the explicitly spatial elements of fluvial geomorphology. Testing these links, the remainder of this article uses the example of two watersheds in Southern California to address the relationship between hydrogeomorphic disturbance and riparian diversity. Specifically, I explore whether the alpha-scale—within-site—diversity of woody riparian vegeta-
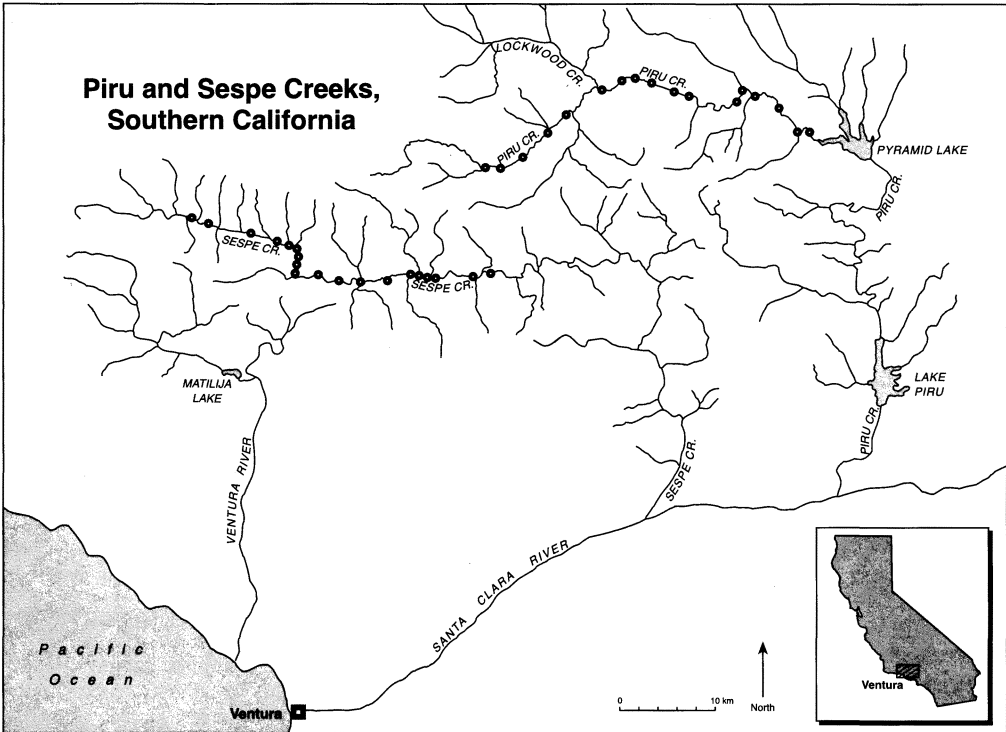
FIG. 3—The study area: Piru and Sespe Creeks in Southern California. The dark circles represent sampling sites.

tion changes systematically through the watersheds and whether the distribution of that diversity can be related to variation in flood intensity.

STUDY AREA

The data are drawn from two watersheds that drain the western Transverse Ranges of California: Sespe and Piru Creeks (Figure 3). The Transverse Ranges are dominated by a complex series of generally eastward-trending structural folds, intersected by numerous compressional and strike-slip faults both parallel to and across the fold axes (Bailey and Jahns 1954). The lithology of the region is also complex: The watersheds drain areas of Cretaceous and Tertiary sedimentary units in some locales; in others they intersect a granitic and gneissic basement complex (Merrill 1954). The extensive deformation of the bedrock in these mountains is of some fluvial significance, because it results in several localized valley reaches where bedrock is exposed at the channel floor. Valley bottoms in these watersheds vary from quite narrow (less than 15 meters) to broad (more than 100 meters). Although most have at least modest alluvial floodplains, at some sites bedrock control imposes steep stream gradients, resulting in high-energy floods.

The area has a Mediterranean climate, with dry summers and cool, wet winters. Most streams in the area have negligible to nonexistent discharges in summer but

may be subject to large floods during frontal storms in winter or early spring, when high-intensity, long-duration precipitation is dropped on steep slopes with shallow soils (Raphael and others 1995).

Riparian vegetation here is dominated by Fremont cottonwood (*Populus fremontii*), white alder (*Alnus rhombifolia*), seep-willow (*Baccharis glutinosa*), and several willow species (*Salix*) (Bendix 1994a). These are often joined on the floodplain and terraces by chaparral species such as chamise (*Adenostoma fasciculatum*) from the surrounding hillslopes.

These watersheds are unusual in the western United States for their absence of grazing impacts. Sespe Creek has been virtually immune to grazing pressure due to limited accessibility and the absence of substantial forage (Borchert 1990), and large portions of the Piru watershed have experienced such light grazing—at least in recent decades— that no measurable impacts on the vegetation can be discerned (Bendix 1994b).

METHODS

An earlier study of riparian species–environment relationships (Bendix 1994a) provided data on vegetation and hydrologic variables. The vegetation data are from line-intercept sampling of woody species conducted at cross-valley transects at thirty-six sites along the main stream in each watershed (Canfield 1941; Greig-Smith 1983). This sampling strategy provided data not only for the number of species present but also linear cover values—readily converted to importance values—amenable to the calculation of measures of diversity. The limitation to woody species reduced any sensitivity of the data to the season of data collection and to inter- and intra-annual variability of a climatically sensitive herbaceous cover.

The calculation of species diversity is complicated somewhat by the multiple definitions of *diversity*, some of which are at substantial variance (Peet 1974 provides a good review of these). The two most common approaches to diversity determine either the number of species—richness—present in a sample, controlling for either the sample area or the number of individuals in it, or heterogeneity of the sample, which incorporates both the number of species and the evenness of their representation in the sample. This analysis employs two measures, the most commonly used formulations for each of these approaches.

The simpler of these is richness, which requires no equation; it is typically a count of the number of species per unit area of sample—except that here the line-intercept data require the substitution of unit length for unit area. The other measure, representing heterogeneity, is the Shannon-Weaver diversity index (H'):

$$H' = -\Sigma p_i \text{Log} p_i \qquad (6)$$

in which p_i is the importance value, or proportion of the sample—relative cover, in this case—belonging to the *i*th species. All subsequent uses here of *richness* refer to species per meter; H' is referred to as *SW diversity*.

Estimates for the hydraulic variables and for the average values of unit stream power at each site were calculated from cross-sectional surveys conducted at the

same time as the vegetation surveys, from topographic maps, and from output of the
HEC–2 computer program. Details of these calculations have been published else-
where (Bendix 1994a).

Relationships among variables are determined by examination of bivariate plots
and the use of ordinary least-squares regression (Griffith and Amrhein 1991). Re-
sults from the latter should be interpreted cautiously, however, given the small sam-
ple sizes involved (seventeen sites in Piru Creek and nineteen in Sespe Creek). The
small number of observations makes these equations particularly sensitive to the
influence of outliers. As a result, I omitted one site that had been used in other stud-
ies (Bendix 1994a, 1994b) because it had only one species; the resulting zero value for
diversity exerted an undue influence on the regressions.

RESULTS AND DISCUSSION

The seventeen sites analyzed in Piru Creek varied in cross-section size from 32 meters
to 124 meters and in the number of species present from two to eight. In the nineteen
Sespe Creek sites, cross-sections ranged from 20 meters to 124 meters, and the
number of species from four to nine. Overall, twenty-eight species were included. Al-
though these species numbers are low relative to those in many diversity studies
(Ricklefs and Schluter 1993), they are comparable to those encountered for woody
species diversity in other riparian studies (Baker 1990b).

When related to drainage area—the measure of position in the watershed—rich-
ness and SW diversity show very different patterns in the two creeks (Figure 4).
There is disparity not only between the watersheds but also in the distribution of
richness as compared with SW diversity.[1] Richness and SW diversity both increase
downstream in the Piru watershed, whereas in Sespe richness actually decreases
downstream, although in that watershed the trends for both richness and SW diver-
sity are weak and statistically nonsignificant.

The difference between the patterns in the two watersheds can largely be ex-
plained by examination of hydrologic conditions. The assumption of systematic
variation in flood impacts is based on equations 3–5. Those equations, however,
were developed to describe channel conditions in alluvial rivers, where running wa-
ter can reshape channel dimensions with relative ease. Piru and Sespe Creeks have
many reaches where they flow directly atop bedrock; along such reaches the channel
is immune to short-term adjustments in slope. Equation 2 suggests that if slope does
not vary according to expectation, neither will stream power.

That suggestion is confirmed in this case. Unit stream power is clearly highly
sensitive to slope in both watersheds (Figure 5, top). But the distribution of slope
(Figure 5, middle) confounds the expectations from average hydraulic geometry
values, as slope actually increases downstream in Piru Creek and varies almost ran-
domly through Sespe Creek. As slope increases in concert with depth and velocity in
the Piru watershed, stream power increases substantially downstream (Figure 5,
bottom). In Sespe Creek the erratic variation of slope results in the equally unpre-
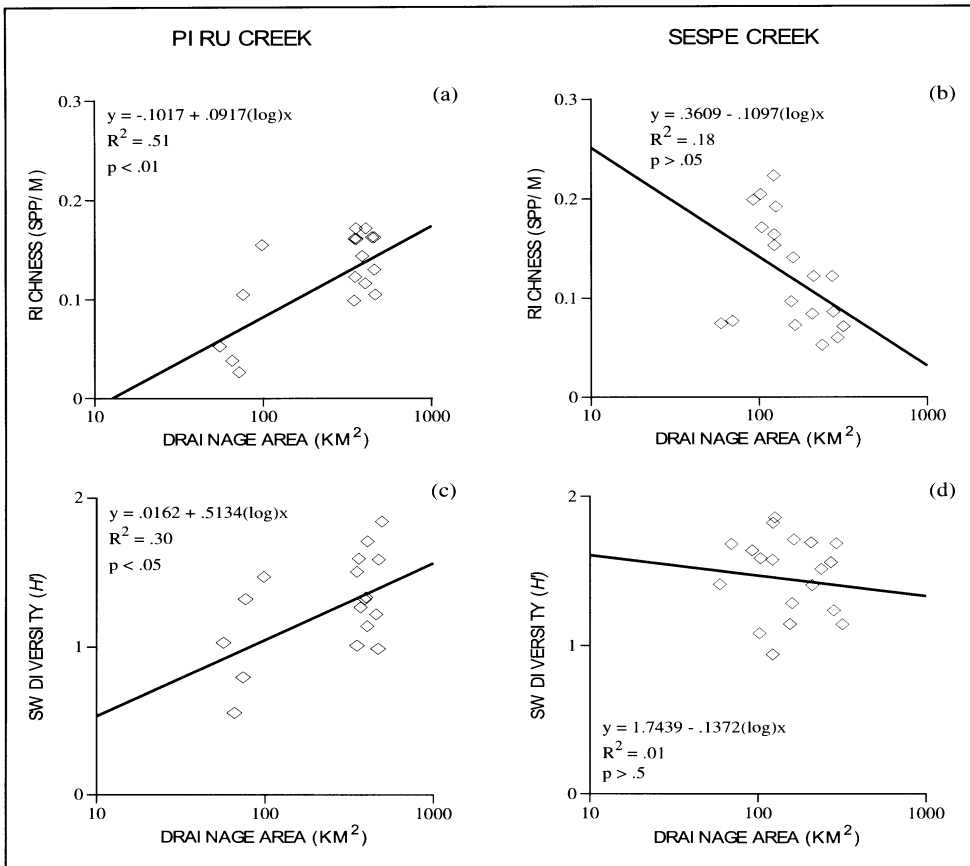dictable distribution of stream power through the watershed.

FIG. 4—The relationship of richness and SW diversity to drainage area: (a) richness × drainage area in Piru Creek; (b) richness × drainage area in Sespe Creek; (c) SW diversity × drainage area in Piru Creek; and (d) SW diversity × drainage area in Sespe Creek.

The hypothesis that richness and SW diversity vary systematically through watersheds was based on the theoretical relationship between diversity and disturbance; it remains to assess the relationship between the diversity measures and stream power. Richness, at least, responds substantially to variation in stream power (Figure 6, top). The downstream increase of stream power in Piru Creek explains an initial finding that richness also increases downstream. In Sespe Creek the random distribution of stream power accounts for a weak relationship between richness and watershed position.

Why, then, does SW diversity (H') not show similar patterns? Its relationship to watershed position is weaker than that of species richness in both watersheds, probably because its relationship to stream power is weaker (Figure 6, bottom). More puzzling yet, the relationship to stream power is different in the two watersheds: positive in Piru; negative in Sespe. A possible explanation for the discrepancy between richness and SW diversity lies in the lesser sensitivity of richness to high-
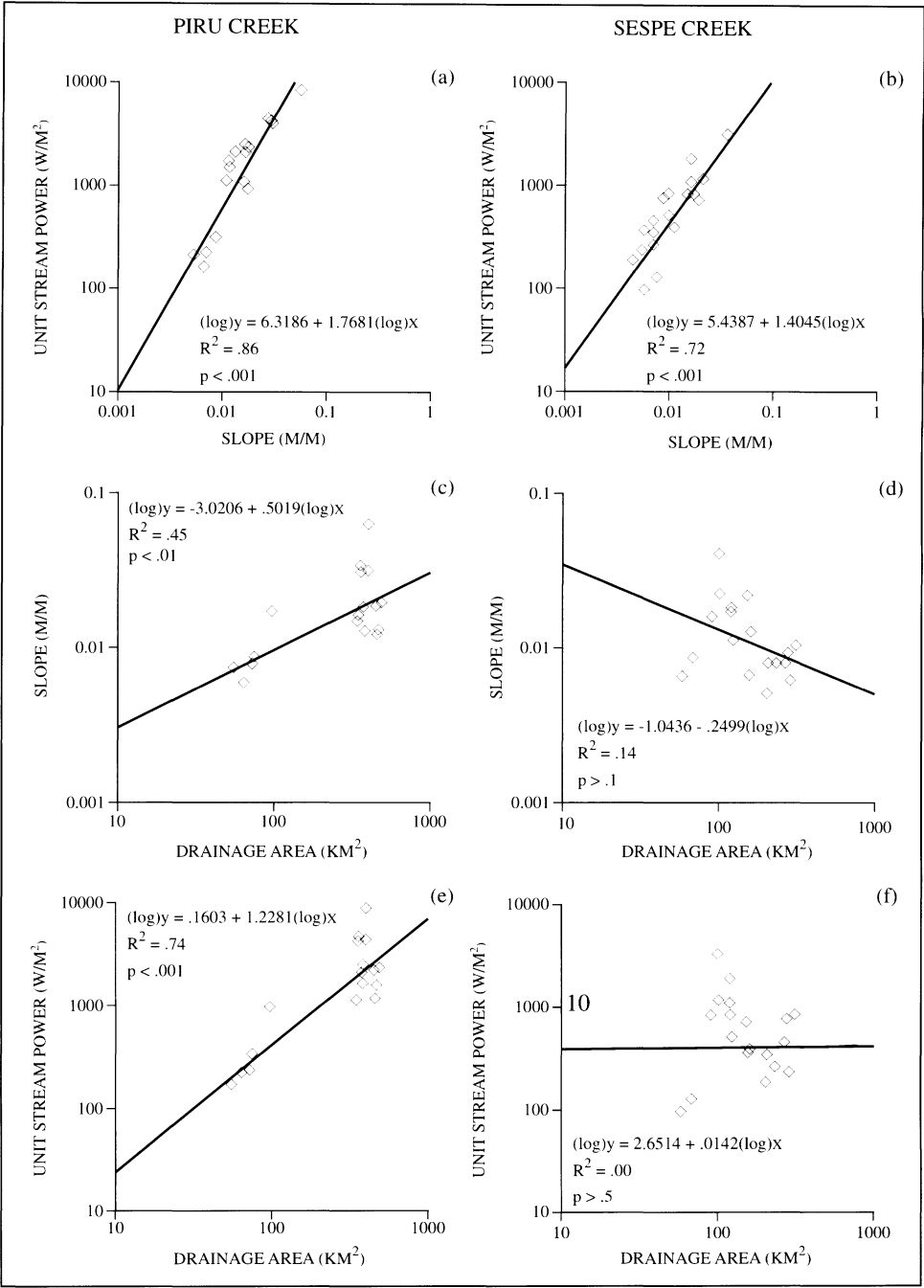
FIG. 5—The relationship of unit stream power to slope, slope to drainage area, and unit stream power to drainage area: (a) unit stream power × slope in Piru Creek; (b) unit stream power × slope in Sespe Creek; (c) slope × drainage area in Piru Creek; (d) slope × drainage area in Sespe Creek; (e) unit stream power × drainage area in Piru Creek; and (f) unit stream power × drainage area in Sespe Creek. The values for unit stream power are for the twenty-year recurrence interval flood.
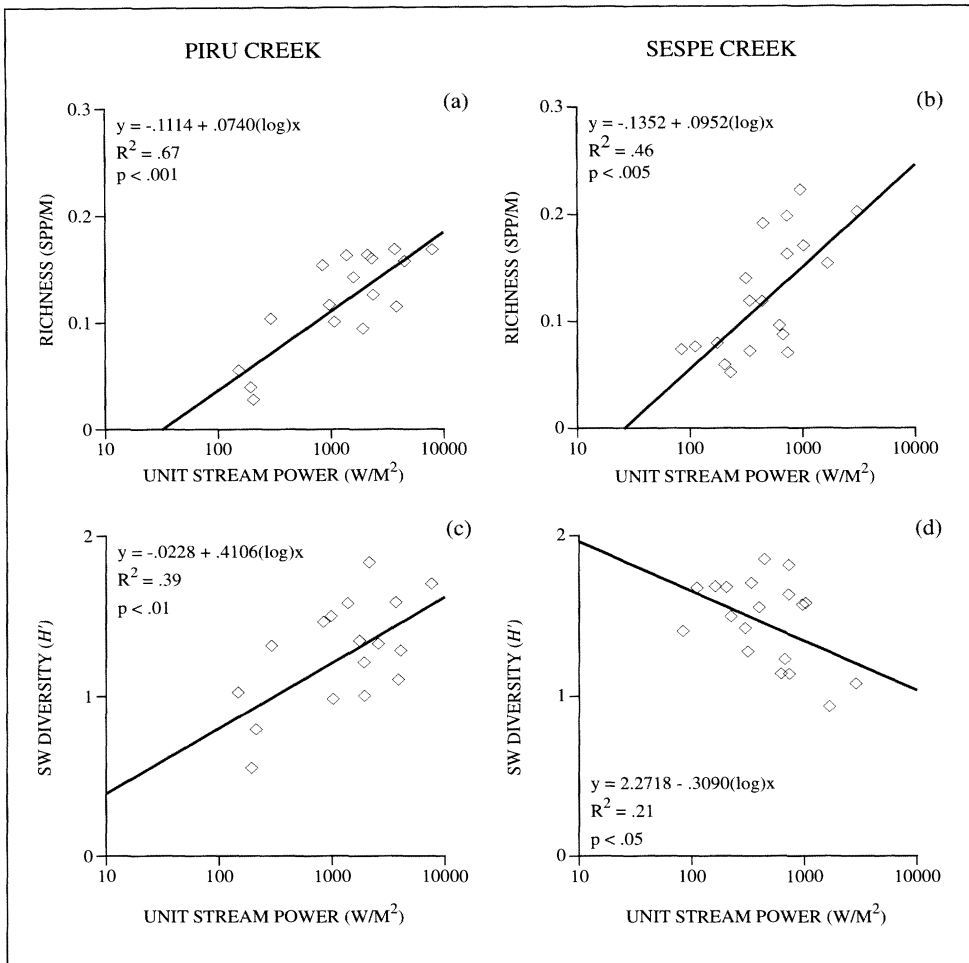
FIG. 6—The relationship of richness and SW diversity to unit stream power: (a) richness × unit stream power in Piru Creek; (b) richness × unit stream power in Sespe Creek; (c) SW diversity × unit stream power in Piru Creek; and (d) SW diversity × unit stream power in Sespe Creek.

magnitude disturbance. A large flood that removes most of a given species from a site will reduce the evenness of the vegetation, and therefore H' will decline. But as long as any representative of the species remains, there is no decrease in richness. This differential response can be illustrated by modification of Figure 1 to allow a single survivor of the high magnitude flood (Figure 7).

Richness can thus continue to increase with increasing disturbance beyond the threshold where SW diversity will decline. In a conceptual sense, this means that the scale of Figure 2a may be different depending on the choice of biodiversity measure; a watershed that falls within A→B when examining richness may actually be within B→C if the Shannon-Weaver diversity index is used.

FLOOD MAGNITUDES   POST-FLOOD VEGETATION

LOW RICHNESS/LOW SW DIVERSITY

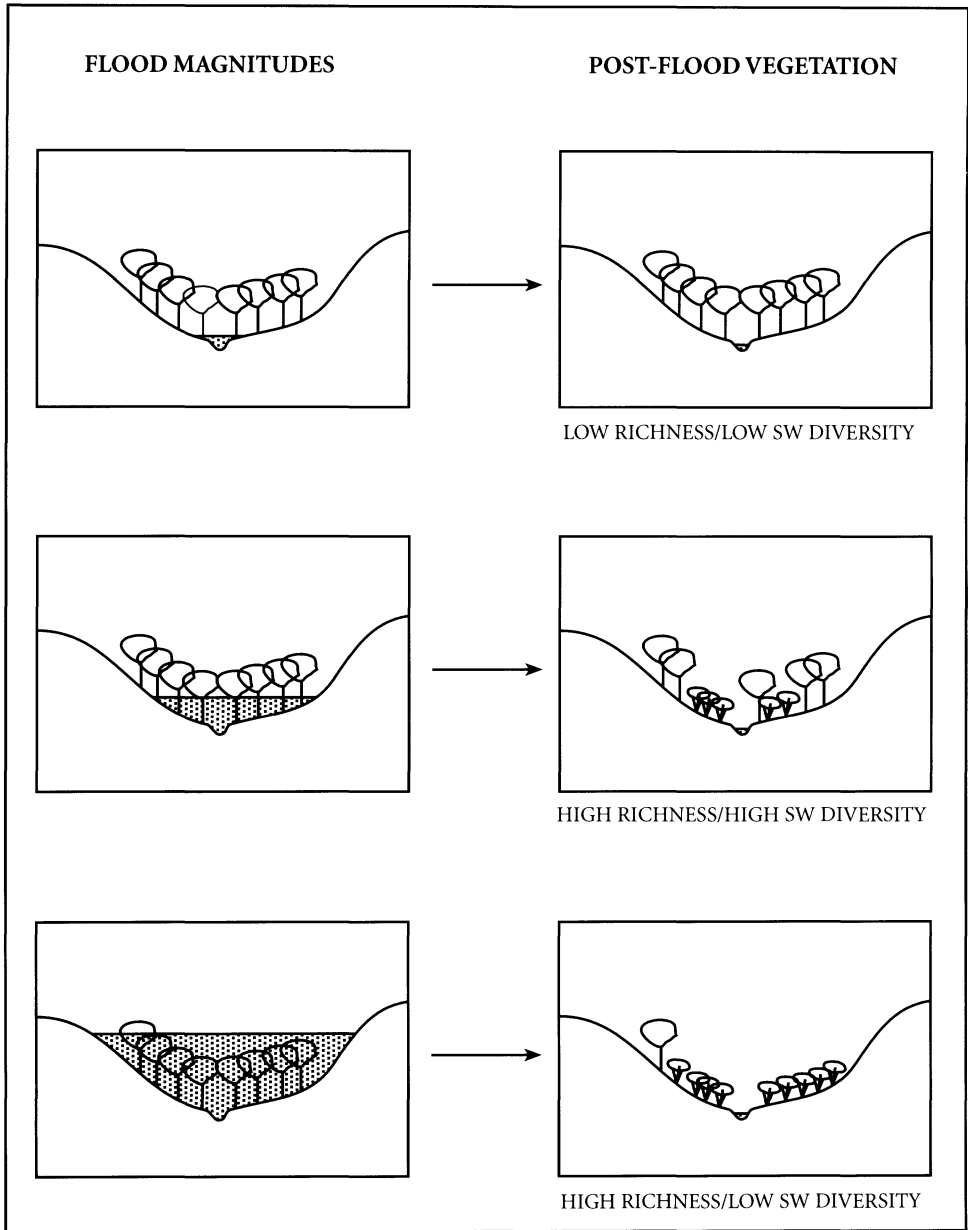HIGH RICHNESS/HIGH SW DIVERSITY

HIGH RICHNESS/LOW SW DIVERSITY

FIG. 7—The differential relationship of richness and diversity to magnitude of disturbance: If any of the preexisting vegetation survives the extreme flood, there is no diminution of richness, but diversity decreases.

CONCLUSIONS

The first question set forth was whether species diversity is distributed systematically through the study watersheds. These data suggest that it is, with two qualifications. One is that the relationship is more clearly seen if species richness is the measure of diversity. The other is that the relationship holds only if hydrologic conditions are also distributed systematically. This is because "yes" also fits the second question: Diversity—especially if measured as richness—is indeed related to flood intensity. Presumably, these relationships would be better expressed in watersheds with purely alluvial channels, where the expectations of hydraulic geometry would be fulfilled (Leopold and Maddock 1953).

Do the several complications encountered in this analysis imply that the theoretical expectations voiced for patterns of riparian diversity are unsound? Quite the contrary: The data indicate that these concepts are useful, but only if applied to a detailed understanding of the local context. As with many other ecological relationships, generalization is possible only to the degree that the underlying assumptions are met. In this case there are multiple assumptions. Some have been explicitly addressed here: The floods routed through watersheds must conform to general hydrologic norms; the range of hydrologic impacts in the watershed must at least partially coincide with the range of ecological vulnerability; the measure of biodiversity must not be "overly" sensitive. Other questions that did not arise in this analysis also merit investigation with more extensive data sets: How much is the pattern of diversity affected by the variation of species composition through a watershed, with its concomitant impact on disturbance vulnerability? How sensitive are diversity patterns to the timing of disturbance, in terms of both the length of time for pioneer species to arrive and the suitability of environmental conditions for their establishment (Baker 1990a)? And how important are interactions among multiple disturbance agents (Savage 1994, 1997)?

Despite the questions that remain, the spatial relationships between hydrologic processes and disturbance-mediated biotic diversity offer intriguing insights into the spatial patterns of diversity. And issues that remain suggest that there are abundant directions for future research in this area.

NOTE

1. Because of the confluence of Lockwood Creek with Piru Creek (Figure 3), there is a notable discontinuity in the drainage area of the Piru Creek sites. Consequently, the regressions for Piru Creek with drainage area as the independent variable should be interpreted with particular caution, because the separation of the data into two clusters may inflate the R^2.

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