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Floodplain plant diversity and conservation in regional and local contexts

Jason E. Mouw
The University of Montana

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FLOODPLAIN PLANT DIVERSITY AND CONSERVATION IN REGIONAL AND LOCAL CONTEXTS

by

Jason E.B. Mouw

M.S.E.S. Alaska Pacific University, Anchorage, Alaska. 1998

B.A. Northwestern College, Orange City, Iowa. 1996

presented in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

The University of Montana

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Approved by:

Chairperson

Dean, Graduate School

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Date

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Floodplain Plant Diversity and Conservation in Regional and Local Contexts

Director: Paul B. Alaback PA

Alluvial floodplains are unique geomorphic features of lotic systems that are characterized by a shifting morphology in three spatial dimensions. This spatial and temporal heterogeneity is thought to explain why these aquatic-terrestrial ecotones are the most species-rich habitats on the terrestrial portions of earth. Many factors and processes influencing these high levels of species richness remain unstudied, however. Regional factors, such as regional species pools, and local factors, such as groundwater-surface water exchange have received little consideration as factors controlling local species richness on floodplains. Additionally, the conservation of these habitats and the biodiversity they support remains shortsighted without the consideration of regional and local factors that influence floodplain structure and function.

A large alluvial floodplain, the Nyack, on the Middle Fork Flathead River, Montana, was used as a study site to investigate the role of the regional species pool in determining local species composition. In this relatively pristine system, our data show that floodplain habitats host 63% of the 320 vascular plants identified within the regional pool, making these habitats the richest in plant species within this catchment. Of these species, 72% are found in at least one adjacent upland habitat indicating a strong local – regional connection; highlighting the importance of the regional species pool in determining local species composition on floodplains.

To investigate the local environmental controls on floodplain plant species richness, both the Nyack floodplain and a large floodplain system on the Talkeetna river, Alaska, were sampled to show that, without exception, species richness gradients are not explained by flooding frequency as commonly thought. On both systems, differences in species richness and productivity between differing floodplain positions were largely a product of groundwater-surface water interaction, where the highest species richness and growth rates of woody plants was found at sites where groundwater is upwelling.

While the conservation of regional plant biodiversity cannot be entirely achieved by merely protecting floodplain habitats, we conclude by proposing a methodology of reserving instream flows to maintain the structure of these habitats, as their physical and floristic diversity functions as critical habitat to faunal assemblages of unparalleled diversity. Flow variability inherent in native flow regimes is required to maintain a spatially and temporally heterogonous fluvially derived landscape.

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PUTTING FLOODPLAIN PLANT SPECIES RICHNESS IN A REGIONAL CONTEXT: AN ASSESSMENT OF TERRESTRIAL – AQUATIC CONNECTIVITY

Abstract. Alluvial floodplains are known to support higher levels of vascular plant species richness than any other terrestrial ecosystem. Whereas the spatio-temporal heterogeneity of these ecosystems has been considered the local determinant of high plant richness, regional influences, such as regional species pools have received little attention. Because high numbers of species congregate on floodplains, these ecosystems are currently considered as critical to the conservation of regional biodiversity. This conclusion, however, has been made without considering the regional biogeography of floodplain plant species. Putting the distribution of floodplain plants within a regional context allows the identification of endemic species and species that are shared with one or more upland ecosystem (*overlap species*) to better define conservation strategies for this critical habitat. This paper investigates the biogeography of floodplain species within Nyack catchment, in Glacier National Park, USA, to estimate the role of upland species pools in determining the species richness of floodplain ecosystems. Our data show that in a pristine system floodplain ecosystems host 202 (63%) of the 320 vascular plants identified within Nyack catchment. Of these species, 146 (72%) are found in at least one adjacent upland ecosystem. Further, of the 146 floodplain species shared with upland ecosystems, 61% of these species were found to be more abundant in upland ecosystems, indicating these ecosystems may be acting as source ecosystems for many floodplain species. Significant levels of endemism were found in floodplain ecosystems (24% of floodplain species), but also within upland ecosystems, where 23% and 40% of low elevation forest and alpine species were found to be endemic, respectively. Whereas 83% of overlap herb species were wind dispersed, <70% of endemic species were animal dispersed, indicating that overlap in species pools may be driven by wind dispersal. These results require the re-evaluation of the contribution of floodplain ecosystems to regional plant species richness. While they host species specific to floodplain ecosystems, other ecosystems have equal or higher levels of regional endemism. Furthermore, these data suggest that conservation of biodiversity on floodplain ecosystems may require consideration of upland ecosystems throughout the catchment, since flood plains may be a sink for many species.

Key words: floodplains, catchment, species pool, connectivity, endemism, conservation.

Introduction

Species richness of plant assemblages within riparian/floodplain ecosystems has been well documented. Many studies have demonstrated unusually high levels of vascular plant species richness on riparian landscapes (Gregory et al. 1991, Nilsson 1992, Tabacchi 1993) leading to the conclusion that riparian corridors are important for the conservation of regional biodiversity (Naiman et al. 1993). Few studies in the temperate zone, however, have actually compared plant species richness levels between riparian and upland ecosystems to show that riparian landscapes are richer in species. The work of Stohlgren et al. 1997 is an exception showing riparian landscapes are richer in plant species than other terrestrial ecosystems in the Rocky Mountain West.

The drivers of this richness in plant species has been of long interest, however, we have yet to sort out the relative roles of regional and local influences to species composition on floodplain ecosystems. In light of the current depauperate state of many floodplain ecosystems due to river regulation and competitive uses of instream flows, the identification of factors and processes that drive the development and maintenance of species rich plant assemblages on riparian landscapes is an urgent objective. Though local species diversity is controlled by a balance between local and regional processes (Ricklefs 1987), studies evaluating regional processes are few. Namely, it has yet to be determined how reflective local species composition on floodplains is reflective of the landscapes their rivers drain. A strong local – regional connection in species pools is thought to exist on river landscapes and explain high plant diversity (Naiman et al. 1993). Species are thought to be added from upland ecosystems due to the migration capacity of plants along riparian corridors, and several studies have investigated this route of dispersal to support this hypothesis (Johansson et al. 1996, Andersson et al. 2000). Though the idea that local floodplain plant assemblages are functionally connected to catchment species pools has been supported in several studies, few studies have investigated overlap in species pools and the population structure of shared species to quantify this functional connectivity. The challenge in addressing this question, however, is to study free-flowing river systems in unfragmented landscapes where patterns in species diversity may be elucidated.

Studies investigating local influences on local species richness on floodplains suggest that high species richness is due to spatio-temporal variability (Pollock et al. 1998, Ward et. al. 1999) as there is a great degree of environmental heterogeneity manifested as micro-topographical variation, substrate heterogeneity, debris complexes, and hydrologic complexity on many riparian landscapes. Alluvial systems are characterized by frequent channel migration mediated by cut and fill alluviation creating great temporal variability. This spatio-temporal heterogeneity greatly increases the number of microhabitats on floodplains, and undoubtedly increases the number of species that can coexist (Pollock et al. 1998, Ward et al. 1999). Also, temporal turnover of habitats promotes a wide array of successional stages, which enhance the diversity of the floodplain and elevate species richness and community diversity.

Floodplains are also characterized by sharp boundaries and gradients that create a variety of ecotones at several scales. At landscape scales, the floodplain itself is an ecotone colonized by a variety of terrestrial, aquatic, and obligate species. Due to the high spatio-temporal heterogeneity on floodplains, many ecotones exist between vegetation patches, kinds of waterbodies (Ward et. al. 1999), and between surface and groundwater (Stanford and Ward 1993). Each ecotone is a zone of mixing and exchange, where properties (thermal, chemical, species composition) from each landscape entity are shared. Because this implies that species are also shared (Naiman and Decamps 1991), the ecotonal nature of floodplains suggests that local species assemblages must reflect the regional species pool.

Because assessments of plant species richness on floodplains have most often focused on the number of species on a given floodplain (gamma diversity) or the number of species per plot (alpha diversity), the ability to quantify connectivity between floodplain and regional species pools is lacking. Some analyses of floodplain animals have focused on endemic species, however, and have shown that riparian ecosystems support more endemic species than upland ecosystems (see Kelsey and West 1998). Floodplain plant species richness, however, is rarely investigated within a regional context to compare patterns of plant species richness on floodplains to adjacent uplands, or evaluate the connectivity of catchment and floodplain species pools across aquatic terrestrial ecotones. Focus on the composition of floodplains and the biogeography of species present is required to quantify levels of endemism and connectivity with upland species pools. Although riparian ecosystems are considered critical in the conservation of regional biodiversity (Naiman et al.

1993), this conclusion may be premature until the connection between local riparian plant communities and regional species pools is understood. That most species in riparian zones are rare (Naiman et. al. 1993, Decamps and Tabacchi 1994) indicates that these ecosystems may not be a source of propagules, but rather species sinks of relatively high spatial and temporal species turnover. If most plant species in riparian zones are shared by upland source ecosystems, floodplain ecosystems may not be as important to the conservation of regional biodiversity as currently thought. Conversely, if a significant percent of species in riparian zones are obligate to these ecosystems, then floodplains should be considered as critical ecosystems for such species, and important to regional biodiversity. Though it has been shown that riparian ecosystems host species specialized to the unique habitats on floodplains (Tabacchi 1992, Nilsson et. al. 1994, Alaback 1995), it has also been shown that 93% of hillslope species occur on the Adour river floodplain of France (Tabacchi 1992). This indicates that these species are general or present in greater abundance in upland ecosystems not associated with lotic systems.

This paper examines where plant species richness, endemism, and species abundances are concentrated within Nyack catchment, a pristine landscape in Glacier National Park, Montana. We assume a local – regional species pool connection, and we determine the extent to which species are shared between aquatic and terrestrial ecosystems throughout this catchment to quantify connectivity between these species pools. We predict that floodplains within Nyack catchment support higher levels of richness and endemism than terrestrial ecosystems. We also predict that species shared between floodplain and terrestrial ecosystems will be relatively rare on floodplains. Upon understanding patterns of endemism and the relative abundances of plant species shared across aquatic-terrestrial ecotones, the contribution of floodplain ecosystems to regional plant species richness can be evaluated.

Methods

Site of Investigation

The distribution and abundance of vascular plant species were observed within the catchment of Nyack Creek, a third order tributary to the Middle Fork of the Flathead River, Montana. Nyack Creek lies entirely within Glacier National Park, flowing southwest from the continental divide at 48°30" N - 113°30" W, elevation 1600 m. to approximately 48°27" N - 113°48" W, at 1100 m. in elevation. It drains several small lakes, glaciers, and snow fields and flows from alpine to low elevation forests, encompassing a variety of forested landscapes. Along this stream are several active alluvial floodplains that were sampled along with the adjacent uplands from valley floor to alpine. Nyack floodplain, a large alluvial reach of the Middle Fork of the Flathead River and located at the confluence of Nyack creek was also sampled. The Middle Fork is a snow-dominated system with great flow variability. Mean annual flow of the Middle Fork, determined by US Geological Survey gauging station (# 12358500) is 82 m^3/s. The Nyack is a large floodplain 9 km in length and 3 km wide at its widest point. The porous alluvium absorbs 20 % of surface flows to alluvial aquifers in the upper 3 km of the floodplain, indicating a strong ground-surface water interaction (Stanford et al. 1994). Sampling occurred along the widest reach of the floodplain, accounting for approximately 4 km^2 of the entire floodplain and centering on the confluence of Nyack creek and Nyack floodplain. Nyack catchment is rarely visited due to difficult access, thus human disturbance on floodplains is not a factor influencing vegetation assemblages. The floodplains on Nyack creek are intensively used throughout the year by whitetail deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*) Rocky Mountain elk (*Cervus edaphus*), as well as black (*Ursus americanus*) and grizzly bear (*Ursus horribilis*).

Sampling Protocol

To determine the regional pool, all vegetated physiognomies of Nyack catchment were sampled. This included floodplain, high and low elevation forests, and alpine ecosystems. Within each ecosystem vegetation was sampled within 50 x 2 m. plots spaced 50 m. apart (Gentry 1982) stratified by elevation, topography, slope, and aspect, to account for as many influences on species composition as possible. Within a given stratum, plots were randomly located, though rare habitats such as slope failures, slides, windthrow, and avalanche chutes were sampled with an additional plot when encountered. Each plot was divided into five 10 x 2 meter plot segments in which the presence of all vascular plants and visual estimates of their percent cover was recorded. Plots were sampled within each ecosystem until all strata were sampled and species area curves reached an asymptote.

Ecosystem descriptions

Sampling of riparian ecosystems was restricted to well-developed alluvial floodplain reaches of Nyack Creek and Nyack floodplain. These stream reaches display the strongest physical aquatic - terrestrial connectivity because seasonal flood flows subject floodplain surfaces to cut and fill alluviation. Conversely, bedrock confined or incised river reaches support relatively narrow bands of floodplain vegetation, and are characterized by upland disturbance regimes (wind, fire, avalanches, etc.). Floodplain reaches were characterized by Cottonwood forests (*Populus balsamifera*) and shrub communities dominated by willow (Salix) species (see Mouw 2000), alder (*Alnus incana*), *Cornus stolonifera*, and *Lonicera involucrata.*

Forested landscapes of Nyack catchment are fire ecosystems. Much of the landscape surrounding the Middle Fork has been colonized by stand replacing lodgepole pine (*Pinus contorta*), with residual patches of larch (*Larix occidentalis*), and even some isolated patches of western red cedar (*Thuja plicata*). North and West facing slopes support Engelman spruce - subalpine fir forests (*Picea engelmannii, Abies lasiocarpa*). Much of the forests of Nyack catchment are characterized by Douglas fir forests (*Pseudotsuga menziesii*), though *Picea - Abies* forests are found on west facing slopes at lower elevations. *Larix* stands occupy small drainages, depressions, and wetter sites. Also present on south facing, well drained sites, is Ponderosa pine (*Pinus ponderosa*). Valley floors are dominated by *Picea - Abies* forests that typically occur in narrow bands and often extend to 1200 m in elevation on west and north facing slopes. In this study, forests above 1200 m are considered as distinct from those forests of lower elevations. These forests are delineated as such to reflect stark differences in species composition and forest structure. With exception of *Larix* stands that occur in both forest types, high elevation forests are shorter in stature and depauperate of species relative to the forests of lower elevations. *Pseudosuga – Larix* and *Pinus* stands dominate high elevation forests, while low elevation forests are dominated by *Picea - Abies* forests.

Typically above 2100 m alpine sites form distinct ecosystems where tree growth becomes physiologically impossible due to slides and winter snow depths. This straightforward delineation of Nyack catchment into these physiognomically distinct ecosystems allows for the determination of the extent in which species are shared across the catchment as a whole.

Species definitions

The species richness of vascular plants on floodplains is composed of two groups of species. There are species that are restricted to particular ecosystem, which will be called *endemic species*, whereas those species that occur in more than one ecosystem, are called *overlap species*. *Overlap species* are often represented by several populations disjunct from one another in two or more ecosystems. The population structure formed by *overlap species* conforms to the conceived and modeled *metapopulation* by Levins (1969), where disjunct populations are envisioned as going through repeated extinctions, and extinction probability decreases with population size. The term metapopulation has been used in a variety of different ways (Hanski and Simberloff 1997). Here we use this term to describe assemblages of populations in spatially distinct ecosystems within Nyack catchment (after Moilanen 1998).

Because endemic and overlap species make different contributions to catchment species diversity, two distinct richness patterns are defined. The contribution significance of an overlap species to gamma diversity is dependent on its abundance within a given ecosystem. An overlap species present at very low levels of abundance may go extinct locally over time, and though re-colonization may be likely, this is dependent on the integrity of a source population where the species can persist without aid from other disjunct population segments. Thus, gamma diversity, or species richness of a given ecosystem is always influenced by overlap species, where the total number of overlap species is called *overlap richness*. Conversely, the total number of endemic species is called *endemic richness*. This partitioning of species richness allows the separate contributions of overlap and endemic species to be understood, and subsequently the patterns of gamma diversity to be evaluated. Often, high species richness, as on floodplains, can be explained by the large number of overlap species contributed from other adjacent ecosystems supporting source populations of these species. Because overlap species are often prone to extinction where they are rare, high overlap richness may indicate that a given ecosystem is not as important for the conservation of regional biodiversity as concentrations of endemism are.

Data Analyses

Initially the data were entered into computer list file and proofread to insure accuracy of transcription. A data matrix was constructed providing the basis for the data analyses described below. Basic univariate statistics were computed to determine average cover values of each plant species, allowing an analysis of variance on mean species abundance within ecosystems and post - hoc multiple comparisons of means (described below in detail).

To determine the distribution of plant species within Nyack catchment, a nested subset incidence matrix (Patterson and Atmar 1986) was constructed (Table 1, also see Appendix). This analysis is a powerful tool used to determine the degree to which species-poor ecosystems are subsets of species-rich ecosystems, and to identify species which are most at risk to extinction. Species - ecosystem matrices are constructed with ecosystems ordered in rows from richest to poorest and species in columns from most to least frequent. A data set exhibiting "perfect nestedness" results in an incidence matrix where all x's are as far to the left and to the top of the matrix as possible (Brualdi et al. 1999). Discrepancies (sensu Brualdi et al. 1999) accrue as species in poorer ecosystems do no occur in the preceding ecosystem of the incidence matrix (see Table 1). In the following analysis we will note discrepancies. however the main questions answered by this analysis relate to how species are distributed across Nyack Creek catchment. Specifically, this analysis is used to determine species richness in each ecosystem, the extent to which floodplain species are shared with upland ecosystems, the number of endemics in each ecosystem, and the number of ecosystems occupied by each species. To conduct this biogeographic analysis, a site-species matrix is constructed where ecosystems are listed from richest to poorest, and species are ordered by their frequency of occurrence.

Differences in species composition

Ordinations of the vegetation data were produced using detrended correspondence analysis (DCA) with equal weight given to all variables and 26 segments used in detrending. This ordination technique was used to visually represent how plots from the six ecosystems group in multivariate space. This analysis begins to ask how similar or dissimilar is the species composition amongst the *a priori* ecosystem groupings. Following the ordination of plots, a multi-response permutation procedures test (MRPP) was conducted. MRPP tests whether the groups formed by plots within each ecosystem significantly deviate from random organization. This analysis is used to simply show whether or not one can distinguish between each of the six ecosystems based on species composition.

Connectivity across ecotones

Species richness can be examined within a plot, a local patch or community, a region, or between sites. Whittaker's (1972) components of diversity allow for the partitioning of diversity into three components, where alpha is richness at the plot level, beta is the degree of differentiation between two samples, and gamma is the sum of alpha diversities over a region. These components allow the contributions of local richness, species niche breadth, and habitat heterogeneity to diversity to be considered (Schluter and Ricklefs 1993). This partitioning of diversity allows for a rigorous comparison of richness on floodplains and uplands, as well as the connection between the two. Most studies of floodplain plant species richness report how these components of diversity vary across a landscape gradient (Gould and Walker 1999), or simply how alpha and gamma on floodplains are extraordinarily high (Naiman et al. 1993). Few studies have investigated beta diversity across the aquatic-terrestrial ecotone to determine similarity between upland and floodplain species lists. Studies have shown how beta can be used to determine how species composition changes along the gradient of connectivity within floodplains (see Ward et. al. 1999). Ward et al. call for beta to be analyzed as a new way of investigating species richness patterns on floodplains. The present study uses beta to determine the degree of connectivity between floodplains and adjacent uplands to determine the influence of each ecosystem on regional biodiversity. Beta is calculated simply as:

$$\beta = \Sigma \text{ unique species in each ecosystem}/\Sigma \text{ of all species in both ecosystems}$$

This gives the turnover rate between two ecosystems (Kikiwa 1998), and can be used when the total number of ecosystems has not been determined, which is required to calculate Whittaker's beta. Determining the number of ecosystems can be very subjective, and should depend upon environmental measurements not vegetation associations (Sheiner 1999, *personal communication*). Thus, in the absence of such a community analysis, turnover rates are simply calculated. Using this metric, two ecosystems with complete turnover (no species shared) would yield a β of 1, whereas ecosystems sharing all species would yield a β of 0.

Life form and Dispersal Analyses

To better understand influences to beta diversity within Nyack catchment, species are grouped by life form and dispersal strategy. These analyses show the relative percent composition of herbs (h), graminoids (g), shrubs (s) and trees (t). In addition, dispersal strategies of these species are analyzed to attempt to recognize mechanisms that provide for connectivity between local species pools. Species with wind-adapted seed are categorized as wind dispersers (w), species with fleshy seeds are considered to be animal dispersed (f), while the remaining species are categorized as "other" (o). Species in the "other" category develop seeds that are not winged and have no other obvious appendages to aid dispersal. It must be noted that many of these species in any category may be water dispersed.

Frequency and Cover Analyses

Dividing the plots into five 10 x 2 m. segments allows the frequency of occurrence for each species to be determined. Frequency of occurrence can used as an index of abundance. Here the average frequency of each species was determined simply by dividing the number of plot segments occupied by a species over the total number of segments *within each ecosystem* it is present to illustrate the metapopulation dynamics of each species (Here, metapopulation dynamics refer to the present distribution of abundances between spatially disjunct populations, not the repeated colonization and extinction of population segments over time). This allowed a determination of where each overlap species occurs most frequently, and how many overlap species on floodplains are more frequently encountered in upland ecosystems.

The average cover of each species was also calculated within each physiognomic group. Cover values were transformed with an arcsine square root transformation and an analysis of variance (ANOVA) was conducted to test if mean abundances of species significantly differed among ecosystems in which they are shared. To test the hypothesis generated from the ANOVA a Tukey-Kramer post hoc comparison of means was conducted to determine if differences are significant, and where each overlap species is most abundant as determined by the percent cover data.

Results

Within Nyack catchment 320 vascular plant species were identified representing 51 families. Floodplain ecosystems were the most species rich, hosting 202 vascular plant species or 63% of all species amongst the three floodplains sampled. Of these 202 species, 164 were found on Nyack floodplain, and 108 and 88 species were found on lower and upper Nyack creek floodplains, respectively (Fig. 1a). At the plot level richness was as high as 70 species per plot with an average of 43 amongst the three floodplains (Fig. 1b). Low elevation forest ecosystems were second in species richness, where 149 species were encountered, or 47% of all species. At the plot level, richness was as high as 49 species with an average of 34 species per plot. Alpine ecosystems were also quite species rich with 137 species or 43% of all species. At the plot level the highest richness was 49, with an average of only 35. High elevation forests were the poorest in species with a total of 79 species encountered or 25% of all species. At the plot level, a maximum of 47 species were recorded with an average of 39. Thus, based on alpha and gamma diversity, these data show floodplains to be the richest in species, as many other studies have shown or suggested. However, looking at alpha and gamma richness, we begin to see the importance of considering beta. For example, the fact that richness at the plot level does not follow the same trend as gamma diversity indicates that beta diversity must be a significant component to overall diversity in high and low elevation forest systems of Nyack catchment. That is, species turnover is high between sample sites in communities with low alpha diversity and high gamma diversity.

Ordination Analyses

A scatter plot of the first two DCA axes reveals some separation of ecosystems based on their species composition (Fig. 2a). All major ecosystem types form distinguishable groupings of plots. Further, the results of the MRPP analysis show that these groupings are significantly different from random, showing that the ordination was successful in separating the ecosystems. The first axis has a corresponding eigenvalue of 0.799, and thus explains 79% of the total variation in species space. This axis appears to most strongly represent a gradient from open/dry sites, to moist sites within a closed canopy. For example, Devils Club (*Oplopanax horridum*) a species with a stong negative score on the first DCA axis colonizes wet *Picea-Abies* forests, while Sandbar willow (*Salix exigua*) which colonizes dry, open sandbars on floodplains occurs on the opposite end of the DCA axis (Figs. 2b and 2c). It is also interesting to note that the species scoring in the central portions of the first axis are overlap species. Red osier dogwood (*Cornus stolonifera*), which scores in the middle of the first axis, occurs in all six ecosytems (Fig. 2d). While the ordination shows that each ecosystem is distinct to some degree, species such as *Cornus s.* weaken the ordination, and show that overlap exists between these species pools.

Nested Subset Analysis

While the above ordination begins to show the distinctiveness of each ecosystem, and that many species must be specific to a particular ecosystem, it is also apparent that there are some species shared amongst two - several ecosystems. For example, the scatterplot (Fig. 2a) seems to indicate that floodplains and alpine ecosystems must be sharing some species, however, it is not readily apparent which or how many species are shared amongst any two species pools. For this question we must investigate the species x ecosystem incidence matrix which specifically identifies the overlap and endemic species, and amongst which ecosystems each overlap species is shared.

First to mention is that the incidence matrix obviously deviates from perfect nestedness (see Appendix). That is, not all ecosystems are found to be subsets of

Nyack floodplain, the richest ecosystem. In fact, there are many discrepancies, which show that some species occurring in upland ecosystems are not found on floodplains. Also adding to these discrepancies, are species from ecosystems that are subsets of the Nyack floodplain, but not found in richer ecosystems preceding them in the incidence matrix. Alpine ecosytems provide for both kinds of discrepancies. For example, we see that alpine ecosystems host many endemic species that create discrepancies. On the other hand, some alpine species are shared with floodplain ecosystems, but are not found in any other ecosystems, making for more discrepancies. Thus, analysis of these discrepancies is a powerful tool in understanding the biogeography of these species. Even though perfect nestedness is not achieved with these data, we can begin to quantify the extent to which any two physiognomic groups share species.

Of the 202 species found on floodplains 146, or 72% were found in at least one adjacent ecosystem as shown by the nested subset analysis for the entire catchment (Appendix). Thus, overlap between floodplain and catchment species pools is quite strong. On Nyack floodplain, for example, 75% of high elevation forest species are present; the highest degree of overlap seen between any two ecosystems. Low elevation forests and alpine ecosystems also contribute 61% and 43% respectively. This connectivity is also exhibited on higher elevation floodplains of Nyack creek. On the upper floodplain 55% of high elevation forest species, 56% low elevation forest, and 49% of alpine species occur on the floodplain. On the lower floodplain, connectivity is the lowest with 57%, 43%, and 33% of high elevation, low elevation forests, and alpine species present, respectively.

Beta Diversity within Nyack Catchment

Beta diversity also revealed the similarity of species pools, or connectivity between each described ecosystem (see Table 2). Turnover among floodplains is lowest, whereas most species overlap all three floodplains in distribution. Turnover is related to distance between floodplains, where the lowest turnover rate is between the two higher elevation floodplains, and the highest between Nyack floodplain and Nyack creek upper floodplain. For comparison, turnover rates between upland species pools are also included, showing much higher turnover rates. The greatest connectivity is seen between low and high elevation forests, and the lowest degree of connectivity seen between alpine and high elevation forests. This is surprising since these species pools are close along the elevational gradient. Also evident from this table is the relative contribution of each upland pool to the floodplain. The highest degree of connectivity across the terrestrial - aquatic ecotone is seen between Nyack creek lower floodplain and low elevation forests (Table 2).

Endemic species

Within Nyack catchment, 148 species are endemic, or 46% of all species. This indicates that endemic richness is significant component to the catchment species pool. Although species richness is the highest on floodplains, the number of endemics is not significantly greater than in other ecosystems. Thus, the greater richness associated with floodplains is explained by species that are shared with upland ecosystems. 56 of 202 floodplain species are endemic to floodplains within Nyack catchment, therefore, 146 species, or 72% of floodplain species are shared with upland ecosystems (Table 3). Alpine ecosystems show a stronger concentration of endemism, with 55 endemics, out of only 137 species. All forest ecosystems contain 44 endemics in a pool of 219 species.

Life form and Dispersal analyses

To investigate differences in species composition, life form and dispersal analyses were used to interpret beta diversity. The majority of species in each physiognomic group are herbs, ranging from 79% of alpine to 57% of high elevation forest species pools (Table 4a). This analysis also helps clarify the turnover rates between ecosystems. For example, the high turnover rate found between alpine and high elevation forests appears to be partly explained by the large differences in species composition by life form. Whereas alpine ecosystems are dominated by herbaceous species, high elevation forests have many more woody species (12% trees, 27% shrub). This analysis also gives further identity to endemic and overlap species. For example of the 40 endemic species to Nyack floodplain, 24 are herbaceous, 10 are grasses, 5 are shrubs and only one is a tree (see Appendix). The majority of overlap species found on Nyack floodplain are also herbs.

Analysis of dispersal strategies also helps explain patterns in connectivity across Nyack catchment (Table 4b). While it is beyond the scope of this paper to fully analyze the dispersal strategies of all species, grouping species into broad dispersal categories yields some interesting patterns. For example, though the majority of all species within each ecosystem are wind dispersed, this percentage is highest for the three floodplains sampled. Of the 40 endemic species on Nyack floodplain 17 are wind dispersed, while the remaining 20 are in the *other* category and 3 are animal dispersed. Analyzing only the herbs, which make up the majority of the endemic species, 71% are not wind dispersed. Conversely, 83% of the overlap species are wind dispersed on Nyack floodplain.

Frequency analysis of riparian plants

The degree of catchment-floodplain connectivity evident with these data brings to question the metapopulation dynamics of overlap species. Of the 146 overlap species on floodplains, 61% are more abundant in upland ecosystems. Results of the ANOVA show that a difference in mean abundance between uplands and floodplains is significant for overlap species ($p < .001$). The Tukey - Kramer post hoc test shows that abundance levels of overlap species are significantly more abundant for only 55% of these species. 22 of 119 (18%) are significantly more abundant on floodplains, while 27 % show no significant difference.

Discussion

In spite of the narrow spatial extent of alluvial floodplains, these ecosystems harbor uncommon levels of vascular plant species richness. Flood plains maintain nearly as many species as all forested ecosystems. Indeed floodplains could be considered as regional centers of organization as they host the majority of species within the landscapes they drain. Environmental correlates of this great richness on floodplains have been identified at the local level, such as substrate fineness and heterogeneity (Nilsson et al. 1989, Nilsson 1992), and microtopographical variation (Pollock 1998). Regional factors, however, are poorly understood, though several hypotheses have been developed and tested such as dispersal along riparian corridors (Nilsson et. al. 1994) allowing for species exchange between regional and local species pools (Decamps and Tabacchi 1994). It is assumed that local richness on floodplains is increased by species migrating from upstream regions and colonizing floodplains (Naimain et al. 1993, Decamps and Tabacchi 1994). Johansson et al. (1996) investigated dispersal abilities of plant species along the riparian corridor and found supporting evidence that plants are added to floodplain communities from upstream regions. Andersson et al. (2000) showed that water dispersal ability and patterns in seed transport in streams explained variation in the diversity of riparian plant assemblages along boreal rivers. Analysis of dispersal strategy in the present paper shows that many (83%) of the overlap species are wind dispersed, though in the present analysis we cannot test the idea that species are added to flood plains from upstream regions.

Biogeographic analyses, however, indicate that many species contributing to floodplain plant richness may result from aquatic-terrestrial connectivity, as all upland ecosystems share species with all floodplain ecosystems. This connectivity supplies floodplains with a higher number of overlap species than endemic species, making overlap richness the most significant component to gamma diversity within floodplains. As indicated by the frequency analysis of overlap species, most are relatively rare on floodplains, or at least more abundant in upland source ecosystems. This suggests that species are being added to floodplains from higher elevations within Nyack catchment and that upland ecosystems may be acting as critical source ecosystems that sustain the unique structural and functional attributes of floodplains. Without some estimate of seedling success for overlap species, we cannot conclude that flood plains are actually a sink for these species. We do show, however, that it cannot be assumed that species on floodplains can persist without seed rain from upland ecosystems.

The separate contributions of overlap and endemic species distinguish two very different patterns of species richness. On floodplains, research has failed to distinguish between species richness due to endemism (*endemic richness*), and the overlapping of species ranges from adjacent ecosystems or even biological provinces (*overlap richness*). On floodplains, species range overlap results in the aggregation of an unusually high number of rare overlap species relative to other ecosystems. Although many are rare within flood plains, they are not rare in adjacent ecosystems. Although one of the prerequisites to attaining conservation priority is rarity (Kerr 1997, Turpie et.al., 2000), the reason for rarity on floodplains may undermine the conservation priority of these ecosystems. It has been the working hypothesis of floodplain ecologists that the establishment of uncommon levels of species richness on floodplains is a result of the unique processes occurring within floodplain ecosystems. The non-equilibrium nature of floodplain ecosystems is mediated mostly by upland and hydrologic disturbance regimes. Flooding continually opens patches available for colonization, and upland disturbances, such as slides, and avalanches may create pathways for upland species to floodplain ecosystems. Because of the availability of open niche space for colonization on floodplains, many upland species arrive by chance and establish. However, because some species arriving in this manner are not adapted to flooding disturbance, their occupation of the floodplain may last only one growing season. Thus, the risk of repeated localized extinction for many of these overlap species may be high, and their occurrence on the floodplain may depend on seed rain from the uplands. This implies that conservation priority should be given to source ecosystems for these species.

One consideration however, is that microhabitats within floodplains may act as critical sites for the bio-production for species not identified in this analysis as floodplain source species. Of the 18% of overlap species found to be more abundant on the floodplains of Nyack catchment, many of these species are critical to wildlife. Moose, (*Alces alces*) find unequaled foraging biomass and stability of willow species on active alluvial floodplains. Other overlap species not found to be more abundant on floodplains as a whole may find source habitats within the floodplain however. For example, gallery floodplain forests are subject to infrequent disturbance and reveal unparalleled growth and production. These within-floodplain hotspots are not as susceptible to fire or windthrow, and are infrequently flooded. Thus, a finer scale analysis of within-floodplain plant community patterns may show these sites as sources of bio-production for some species. Studies are needed to investigate the distribution, abundance, and species richness patterns within floodplain ecosystems within a regional context. Subjective delineations of the floodplain based on plant cover should not drive such an analysis however, as sites with similar species composition are likely to function as determined by their physical template. Studies should be conducted such that delineations of within-floodplain habitats allow for predictions of plant community response. Nonetheless, studies have not been conducted in this manner, and to date, researchers have made conclusions on the regional role of floodplains based on floodplain richness as a whole without a consideration for the biogeography of species present.

Floodplain ecosystems have been recognized as important for the conservation of regional biodiversity because of their richness, not the levels of endemism. Others have simply looked at alpha and gamma diversity, and have ignored the catchment-floodplain connection. Because the richness is mostly due to overlap species, these ecosystems may not maintain 70-90% of all species over time, they may just temporarily host many of these species. Because of this we must re-evaluate the contribution of floodplains to regional plant biodiversity. Although it is still uncertain whether species richness or endemism should receive conservation priority (Turpie et. al. 2000), the spatial and temporal turnover of species on floodplains indicates that endemic richness should receive priority within Nyack catchment. As for endemic richness, floodplain ecosystems are not as rich as upland ecosystems. In fact, a greater concentration of endemics can be found in alpine ecosystems, which are not often noted for their contribution toward regional biodiversity. Thus, floodplain ecosystems are no more important than other ecosystems for regional biodiversity. This is not to say these ecosystems are not important, for they make a significant contribution to regional biodiversity. Not only do they host a comparable number of endemic species relative to other ecosystems, floodplains are endangered ecosystems (Naiman et. al. 1993). River regulation has left the world with few uncompromised floodplains on free-flowing rivers, making river restoration and the conservation of active floodplains a priority. The caveat is that floodplains cannot carry regional species diversity without recognizing the important contributions of upland ecosystems.

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Appendix I: Nested Subset Analysis, Nyack Catchment

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of ecosystems
Betulaceae	*Alnus tenuifolia*	w	s	X	X	X	X	X	X	6
Compositae	*Arnica cordifolia*	w	h	X	X	X	X	X	X	6
Campanulaceae	*Campanula rotundiflora*	o	h	X	X	X	X	X	X	6
Cornaceae	*Cornus stolonifera*	f	s	X	X	X	X	X	X	6
Rosaceae	*Frageria virginiana*	f	h	X	X	X	X	X	X	6
Rubiaceae	*Galium boreale*	f	h	X	X	X	X	X	X	6
Umbelliferae	*Osmorhiza berteroi*	w	h	X	X	X	X	X	X	6
Pyrolaceae	*Pyrola secunda*	o	h	X	X	X	X	X	X	6
Rosaceae	*Rubus parviflora*	f	s	X	X	X	X	X	X	6
Ranunculaceae	*Thalictrum sparsiflorum*	w	h	X	X	X	X	X	X	6
Aceraceae	*Acer glabrum*	w	s	X	X		X	X	X	5
Compositae	*Achillea millefolium*	w	h	X	X	X	X	X		5
Ranunculaceae	*Actea rubra*	f	s	X	X	X		X	X	5
Compositae	*Adenocaulon bicolor*	w	h	X	X		X	X	X	5
Rosaceae	*Amelanchier alnifolia*	f	s	X	X		X	X	X	5
Compositae	*Artemesia ludoviciana*	w	h	X	X	X	X	X		5
Compositae	*Aster foliaceus*	w	h	X	X		X	X	X	5
Compositae	*Aster laevis*	w	h	X		X	X	X	X	5
Scrophulariaceae	*Castilleja miniata*	o	h	X	X	X	X	X		5
Cornaceae	*Cornus canadensis*	f	h	X	X	X	X		X	5
Gramineae	*Elymus spp.*	w	g	X		X	X	X	X	5
Onagraceae	*Epilobium anagallidifolium*	o	h	X	X	X	X	X		5
Onagraceae	*Epilobium latifolia*	o	h	X	X	X	X	X		5
Rubiaceae	*Galium triflorum*	f	h	X	X		X	X	X	5
Umbelliferae	*Heracleum maximum*	w	h	X	X	X	X	X		5
Compositae	*Hieracium albiflorum*	w	h	X	X	X		X	X	5
Pinaceae	*Larix occidentalis*	w	t	X	X		X	X	X	5
Caprifoliaceae	*Lonicera dioica*	f	s	X	X	X		X	X	5
Berberidaceae	*Mahonia repens*	f	s	X	X		X	X	X	5
Pinaceae	*Picea engalmanii*	w	t	X	X		X	X	X	5
Pinaceae	*Picea glauca*	w	t	X	X		X	X	X	5
Orchidaceae	*Planthera dialata*	o	h	X	X	X	X	X		5
Pinaceae	*Pseudotsuga mensiezii*	w	t	X	X		X	X	X	5

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Rosaceae	*Rosa woodsii*	f	s	X	X		X	X	X	5
Rosaceae	*Rubus ideas*	f	s	X	X	X	X	X		5
Liliaceae	*Smilacina stellata*	f	h	X	X		X	X	X	5
Rosaceae	*Spirea betulifolia*	w	s	X	X	X		X	X	5
Caprifoliaceae	*Symphorocarpos albus*	f	s	X	X		X	X	X	5
Violaceae	*Viola canadensis*	o	h	X	X		X	X	X	5
Violaceae	*Viola orbiculata*	o	h	X	X		X	X	X	5
Pinaceae	*Abies lasiocarpa*	w	t	X	X		X		X	4
Liliaceae	*Allium cernuum*	o	h	X	X	X	X			4
Compositae	*Anaphalis margaitacea*	w	h	X		X	X	X		4
Umbelliferae	*Angelica arguta*	w	h	X		X	X	X		4
Ranunculaceae	*Aquilegia flavescens*	w	h		X	X	X	X		4
Araliaceae	*Aralia nudicaulis*	f	h	X	X		X		X	4
Leguminosae	*Astragalus tenellus*	o	h	X	X	X		X		4
Compositae	*Cirisium arvense*	w	h	X	X		X	X		4
Compositae	*Cirisium undulatum*	w	h	X	X		X	X		4
Ranunculaceae	*Clemantis occidentalis*	w	h	X	X			X	X	4
Liliaceae	*Clintonia uniflora*	f	h		X		X	X	X	4
Liliaceae	*Disporum hookerii*	f	h	X	X			X	X	4
Gramineae	*Festuca spp.*	w	g	X	X		X		X	4
Rubiaceae	*Galium aparine*	f	h	X	X		X		X	4
Orchidaceae	*Goodyera oblongifolia*	o	h	X	X			X	X	4
Polypodiaceae	*Gymnocarpum dryopterus*	w	h	X	X		X		X	4
Leguminosae	*Lathyrus ochroleucus*	o	h	X	X		X		X	4
Scrophulariaceae	*Pedicularis bracteosa*	o	h	X	X	X	X			4
Gramineae	*Poa spp.*	w	g	X		X	X	X		4
Pyrolaceae	*Pyrola uniflora*	o	h		X	X		X	X	4
Grossulariaceae	*Ribes lacustre*	f	s		X	X	X	X		4
Salicaceae	*Salix bebbsiana*	w	s	X		X	X	X		4
Umbelliferae	*Sanicula marilandica*	w	h	X	X		X		X	4
Compositae	*Senecio triangularis*	w	h	X	X	X	X			4
Compositae	*Solidago canadensis*	w	h	X		X	X	X		4
Liliaceae	*Streptopus amplexifolus*	f	h	X	X		X		X	4

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Saxifragaceae	*Tiarella trifoliata*	o	h		X	X	X		X	4
Liliaceae	*Trillium ovatum*	o	h		X		X	X	X	4
Labiatae	*Vicia americana*	o	h	X	X		X	X		4
Gramineae	*Agopyron spicatum*	w	g	X		X	X			3
Compositae	*Agoseris aurantiaca*	w	h	X		X		X		3
Compositae	*Aster conspicuus*	w	h	X		X		X		3
Compositae	*Aster modestus*	w	h	X		X	X			3
Betulaceae	*Betula papyrifera*	w	t	X			X	X		3
Gramineae	*Calamagrostis canadensis*	w	g	X			X		X	3
Ericaceae	*Chimaphila umbellata*	o	s		X			X	X	3
Liliaceae	*Disporum trachiocarpum*	f	h	X	X		X			3
Rosaceae	*Dryas drummondii*	w	s	X		X	X			3
Polypodiaceae	*Dryopteris expansa*	w	h		X		X		X	3
Equisetaceae	*Equisetum arvense*	w	h	X	X		X			3
Equisetaceae	*Equisetum hyemale*	w	h	X			X	X		3
Compositae	*Erigeron peregrinus*	w	h			X		X	X	3
Rosaceae	*Geum macrophylum*	w	h		X	X	X			3
Compositae	*Heterotheca villosa*	w	h	X			X	X		3
Compositae	*Hieracium gracile*	w	h	X		X	X			3
Hypericaceae	*Hypericum perforatum*	o	h	X	X		X			3
Juncaceae	*Juncus balticus*	w	g		X	X		X		3
Cupressaceae	*Juniperus horizontalis*	w	s		X	X		X		3
Caprifoliaceae	*Linnaeae borealis*	o	h		X	X			X	3
Orchidaceae	*Listera cordata*	o	h	X	X				X	3
Caprifoliaceae	*Lonicera involucrata*	f	s			X	X	X		3
Labiatae	*Mentha arvense*	o	h	X	X		X			3
Ericaceae	*Menziesia ferriguneae*	w	s		X	X			X	3
Araliaceae	*Oplopanax horridum*	f	s		X		X		X	3
Saxifragaceae	*Paxistima myrsinites*	o	s		X			X	X	3
Scrophulariaceae	*Penstomen procerus*	o	h	X	X	X				3
Compositae	*Petasites frigidus*	w	h	X		X	X			3
Gramineae	*Phleum alpinum*	w	g	X		X	X			3
Polypodiaceae	*Polystichum lonchitis*	w	h		X	X	X			3

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Salicaceae	*Populus balsamifera*	w	t	X			X	X		3
Labiatae	*Prunella vulgaris*	o	h	X			X	X		3
Polypodiaceae	*Pteridium aquilinum*	w	h		X		X		X	3
Pyrolaceae	*Pyrola asarifolia*	o	h	X	X	X				3
Pyrolaceae	*Pyrola chlorantha*	o	h		X			X	X	3
Ranunculaceae	*Ranunculus uncinatua*	w	h	X	X		X			3
Rosaceae	*Rosa acicularis*	f	s	X	X				X	3
Elaeagnaceae	*Sheperdia canadensis*	f	s	X				X	X	3
Liliaceae	*Smilacina racemosa*	f	h	X	X		X			3
Rosaceae	*Sorbus scopulina*	f	s		X	X			X	3
Taxaceae	*Taxus brevifolia*	f	t	X	X				X	3
Cupressaceae	*Thuja plicata*	w	t	X	X				X	3
Compositae	*Tragopogon dubius*	w	h	X	X		X			3
Urticaceae	*Urtica dioica*	w	h		X	X	X			3
Liliaceae	*Veratrum viride*	o	h		X	X	X			3
Gramineae	*Agopyron repens*	w	g	X				X		2
Gramineae	*Agrostis gigantea*	w	g	X			X			2
Liliaceae	*Allium textile*	o	h	X	X					2
Ranunculaceae	*Anemone multifida*	w	h	X		X				2
Compositae	*Antennaria alpina*	w	h	X	X					2
Compositae	*Antennaria racemosa*	w	h				X		X	2
Ericaceae	*Arctostaphylos uva-ursi*	f	s				X		X	2
Compositae	*Arnica chamissonis*	w	h		X				X	2
Compositae	*Artemesia frigida*	w	h			X	X			2
Compositae	*Aster sibiricum*	w	h	X		X				2
Ophioglossaceae	*Botrychium virginianum*	w	h	X				X		2
Liliaceae	*Calochortus apiculatus*	o	h		X	X				2
Onagraceae	*Circaea alpina*	f	h		X		X			2
Compositae	*Cirisium hookerianum*	w	h			X		X		2
Orchidaceae	*Corallorhiza maculata*	o	h	X				X		2
Polypodiaceae	*Cystopterus fragilis*	w	h		X	X				2
Compositae	*Erigeron glabellus*	w	h	X	X					2
Gramineae	*Festuca campestris*	w	g		X		X			2

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Rosaceae	*Frageria vesca*	f	h	X	X					2
Liliaceae	*Fritillaria pudica*	w	h	X		X				2
Saxifragaceae	*Heuchera cylindrica*	o	h			X		X		2
Compositae	*Leucanthemum vulgare*	w	h	X	X					2
Leguminosae	*Lupinus parviflorus*	o	h			X	X			2
Leguminosae	*Lupinus sericeus*	o	h		X				X	2
Leguminosae	*Medicago lupulina*	o	h	X		X				2
Leguminosae	*Melilotus alba*	o	h	X			X			2
Boraginaceae	*Mertensia paniculata*	o	h	X					X	2
Scrophulariaceae	*Penstomen albertinus*	o	h		X	X				2
Scrophulariaceae	*Penstomen confertus*	o	h	X	X					2
Rosaceae	*Physocarpus malvaceus*	w	s	X	X					2
Polygonaceae	*Plantago major*	o	h	X			X			2
Rosaceae	*Potentilla diversiflora*	w	h		X	X				2
Rosaceae	*Potentilla fruticosa*	w	h			X		X		2
Pyrolaceae	*Pyrola minor*	o	h	X	X					2
Grossulariaceae	*Ribes oxyacanthoides*	f	s		X			X		2
Cruciferae	*Rorippa palustris*	o	h	X		X				2
Polygonaceae	*Rumex acetosella*	w	h	X			X			2
Salicaceae	*Salix candida*	w	s	X				X		2
Salicaceae	*Salix commutata*	w	s	X			X			2
Salicaceae	*Salix exigua*	w	s	X			X			2
Salicaceae	*Salix glauca*	w	s	X			X			2
Salicaceae	*Salix monticola*	w	s	X			X			2
Salicaceae	*Salix myrsinites*	w	s	X				X		2
Saxifragaceae	*Saxifraga bronchialis*	o	h	X		X				2
Crassulaceae	*Sedum lanceolatum*	o	h		X	X				2
Compositae	*Senecio conterminus*	w	h			X		X		2
Compositae	*Senecio pauciflorus*	w	h		X	X				2
Compositae	*Senecio pseudaureus*	w	h	X			X			2
Caryophyllaceae	*Silene menziesii*	o	h	X		X				2
Caryophyllaceae	*Silene vulgaris*	o	h	X	X					2
Compositae	*Solidago spathulata*	w	h			X			X	2

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Compositae	*Sonchus arvensis*	w	h	X			X			2
Caryophyllaceae	*Stellaria spp*	o	h		X	X				2
Liliaceae	*Stenanthium occidentale*	o	h		X	X				2
Ericaceae	*Vaccinium globularea*	f	s			X			X	2
Ericaceae	*Vaccinium membranaceum*	f	s		X				X	2
Violaceae	*Viola adunca*	o	h	X					X	2
Liliaceae	*Xerophyllum tenax*	o	h		X				X	2
Gramineae	*Agopyron spp.*	w	g	X						1
Liliaceae	*Allium brevistylum*	o	h		X					1
Liliaceae	*Allium schoenoprasum*	o	h			X				1
Betulaceae	*Alnus crispa*	w	s		X					1
Ranunculaceae	*Anemone drummondii*	w	h			X				1
Ranunculaceae	*Anemone occidentalis*	w	h			X				1
Apocynaceae	*Apocynum sibiricum*	w	h						X	1
Ranunculaceae	*Aquilegia formosa*	w	h			X				1
Cruciferae	*Arabis hursuta*	o	h			X				1
Cruciferae	*Arabis lemmonii*	o	h			X				1
Caryophyllaceae	*Arenaria capillaris*	o	h			X				1
Compositae	*Arnica latifolia*	w	h		X					1
Compositae	*Arnica mollis*	w	h					X		1
Compositae	*Artemesia arctica*	w	h			X				1
Asclepiadaceae	*Asclepias speciosa*	w	h	X						1
Leguminosae	*Astragalus alpinus*	o	h			X				1
Leguminosae	*Astragalus spp.*	o	h	X						1
Polypodiaceae	*Athyrium filix-femina*	w	h		X					1
Gramineae	*Bromus inermis*	w	g	X						1
Gramineae	*Bromus spp.*	w	g		X					1
Gramineae	*Brya humilis*	w	g			X				1
Umbelliferae	*Bupleurum americanum*	o	h		X					1
Orchidaceae	*Calypso bulbosa*	o	h						X	1
Liliaceae	*Camassia quamash*	o	h		X					1
Cruciferae	*Cardamine pensylvanica*	o	g	X						1
Cyperaceae	*Carex disperma*	w	g	X						1

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Cyperaceae	*Carex geyeri*	w	g		X					1
Cyperaceae	*Carex haydeniana*	w	g	X						1
Cyperaceae	*Carex phaeocephala*	w	g			X				1
Cyperaceae	*Carex rupestris*	w	g		X					1
Cyperaceae	*Carex spp.*	w	g		X					1
Cyperaceae	*Carex urticulata*	w	g	X						1
Scrophulariaceae	*Castilleja rhexifolia*	o	h			X				1
Compositae	*Centaurea biebersteinii*	w	h	X						1
Caryophyllaceae	*Ceratstrim arvense*	o	h		X					1
Umbelliferae	*Cicuta douglasii*	w	h			X				1
Scrophulariaceae	*Collinsia parviflora*	o	h		X					1
Compositae	*Crepis acuminata*	w	h		X					1
Compositae	*Crepis elegans*	w	h	X						1
Rosaceae	*Cretaegus douglasii*	f	s	X						1
Rosaceae	*Cretaegus rivularis*	f	s	X						1
Orchidaceae	*Cypripedium montanum*	o	g	X						1
Ranunculaceae	*Delphinium glaucum*	o	h			X				1
Ranunculaceae	*Delphinium nuttallianum*	o	h			X				1
Rosaceae	*Dryas octopetala*	w	s			X				1
Polypodiaceae	*Dryopteris arguta*	w	h		X					1
Onagraceae	*Epilobium angustifolium*	o	h	X						1
Onagraceae	*Epilobium ciliatum*	o	h			X				1
Compositae	*Erigeron acris*	w	h	X						1
Compositae	*Erigonum flavum*	w	h			X				1
Polygonaceae	*Eriogonum umbellatum*	w	h			X				1
Liliaceae	*Erythronium grandiflorum*	o	h						X	1
Compositae	*Eupatorium maculatum*	w	h			X				1
Liliaceae	*Fritillaria*	o	h			X				1
Gentianaceae	*Gentiana glauca*	o	h			X				1
Geraniaceae	*Gerainium viscosissimum*	o	h		X					1
Rosaceae	*Geum rivale*	w	h		X					1
Leguminosae	*Glycyrrhiza lepidota*	o	h	X						1
Boraginaceae	*Hackelia floribunda*	o	h			X				1

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Leguminosae	*Hedysarum sulphurescens*	o	h	X						1
Compositae	*Heliomeris multiflora*	w	h			X				1
Umbelliferae	*Heracleum lanatum*	w	h		X					1
Saxifragaceae	*Heuchera parvifolia*	o	h		X					1
Compositae	*Hieracium umbellatum*	w	h					X		1
Hypericaceae	*Hypericum majus*	o	h	X						1
Hypericaceae	*Hypericum scouleri*	o	h					X		1
Leguminosae	*Astragulus spp.*	o	h			X				1
Boraginaceae	*Lithospermum ruderale*	o	h			X				1
Umbelliferae	*Lomatium triternatum*	o	h		X					1
Juncaceae	*Luzula spicata*	w	g			X				1
Juncaceae	*Luzula spp*	w	g	X						1
Leguminosae	*Melilotus offitionale*	o	h	X						1
Polemoniaceae	*Microsteris gracilis*	o	h		X					1
Scrophulariaceae	*Mimulus lewisii*	o	h			X				1
Caryophyllaceae	*Minuarta obtusiloba*	o	h			X				1
Saxifragaceae	*Mitella nuda*	o	h		X					1
Saxifragaceae	*Mitella pentandra*	o	h	X						1
Labiatae	*Monarda menthaefolia*	o	h					X		1
Gramineae	*Muhlenbergia montana*	w	g	X						1
Boraginaceae	*Myosotis alpestris*	o	h			X				1
Boraginaceae	*Myosotis asiatica*	o	h			X				1
Umbelliferae	*Osmorhiza occidentalis*	w	h		X					1
Compositae	*Oxyria digyna*	w	h			X				1
Celastraceae	*Parnassia fimbriata*	f	h			X				1
Scrophulariaceae	*Penstomen eriantherus*	o	h			X				1
Scrophulariaceae	*Penstomen fruiticosus*	o	s					X		1
Scrophulariaceae	*Penstomen lyallii*	o	h	X						1
Hydrophyllaceae	*Phacelia hastata*	o	h			X				1
Gramineae	*Phalaris arundinacea*	w	g		X					1
Hydrangeaceae	*Philadelphus lewisii*	o	s	X						1
Ericaceae	*Phyllodoce empetriformis*	f	s				X			1
Ericaceae	*Phyllodoce empetriformis*	f	s			X				1

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Pinaceae	*Pinus contorta*	w	t						X	1
Pinaceae	*Pinus monticola*	w	t						X	1
Pinaceae	*Pinus ponderosa*	w	t		X					1
Orchidaceae	*Planthera hyperborea*	o	h	X						1
Orchidaceae	*Planthera orbiculata*	o	h						X	1
Polygonaceae	*Polygonum bistortoides*	o	h			X				1
Rosaceae	*Potentilla glaucophylla*	w	h		X					1
Rosaceae	*Potentilla gracilis*	w	h		X					1
Labiatae	*Prunella vulgaris*	o	h	X						1
Rosaceae	*Prunus pensylvanica*	f	t	X						1
Ranunculaceae	*Ranunculus acris*	w	h	X						1
Ranunculaceae	*Ranunculus alismifolius*	w	h	X						1
Ranunculaceae	*Ranunculus eschscholtzii*	w	h			X				1
Grossulariaceae	*Ribes glandulosum*	f	s		X					1
Grossulariaceae	*Ribes hudsonianum*	f	s		X					1
Rosaceae	*Rosa acicularis*	f	s		X					1
Polygonaceae	*Rumex aquaticus*	w	h	X						1
Salicaceae	*Salix dummondiana*	w	s	X						1
Salicaceae	*Salix arctica*	w	s			X				1
Salicaceae	*Salix farriae*	w	s				X			1
Salicaceae	*Salix planifolia*	w	s	X						1
Salicaceae	*Salix scouleriana*	w	s	X						1
Saxifragaceae	*Saxifraga lyalii*	o	h			X				1
Saxifragaceae	*Saxifraga occidentalis*	o	h			X				1
Saxifragaceae	*Saxifraga rhoboidea*	o	h			X				1
Cyperaceae	*Scirpus spp.*	w	g	X						1
Caryophyllaceae	*Silene uralensis*	o	h				X			1
Cruciferae	*Smelowskia calycina*	o	h			X				1
Rosaceae	*Spirea densiflora*	w	s			X				1
Caryophyllaceae	*Stellaria calycantha*	o	h		X					1
Caryophyllaceae	*Stellaria logipes*	o	h			X				1
Caprifoliaceae	*Symphorocarpos oreophilus*	f	s					X		1

Family	Species	Dispersal strategy	Life form	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests	# of habitats
Compositae	*Taraxicum officianale*	w	h					X		1
Ranunculaceae	*Thalictrum alpinum*	w	h			X				1
Liliaceae	*Tofieldia glutinosa*	o	h			X				1
Anacardiaceae	*Toxicodendron radicans*	f	s		X					1
Leguminosae	*Trifolium longipes*	o	h	X						1
Leguminosae	*Trifolium pratense*	o	h	X						1
Leguminosae	*Trifolium repens*	o	h	X						1
Compositae	*Trimorpha acris*	w	h			X				1
Ranunculaceae	*Trollius laxus*	w	h			X				1
Pinaceae	*Tsuga heterophylla*	w	t		X					1
Ericaceae	*Vaccinium cespitosum*	f	s			X				1
Ericaceae	*Vaccinium scoparium*	f	s			X				1
Valerianaceae	*Valeriana sitchensis*	w	h			X				1
Valerianaceae	*Valeriana sitchensis*	w	h			X				1
Liliaceae	*Veratrum viride*	o	h			X				1
Scrophulariaceae	*Verbascum thapsus*	o	h	X						1
Scrophulariaceae	*Veronica americana*	o	h	X						1
Violaceae	*Viola glabella*	o	h		X					1
Compositae	*Wyethia amplexicaulis*	w	g		X					1
Liliaceae	*Zigadensis elegans*	o	h			X				1
Umbelliferae	*Zizia aptera*	w	h				X			1
Elaeagnaceae	*Elaeagnus commutata*	o	h	X						1
Ericaceae	*Rhododendron albiflorum*	o	h		X					1
Ranunculaceae	*Caltha leptosepala*	o	h				X			1

Table 1. Biogeographic analysis of hypothetical data set for 7 habitats and 10 species. Note the sites are ordered by species richness, and species by total occurrence. In this example, species poor habitats are nested within the richer habitats, however note the two discrepancies (see text).

	Site ID							Total Species Number
Species ID	2	1	3	4	5	7	6	
H	x	x	x	x	x	x	x	7
K	x	x	x	x	x	x	x	7
B	x	x	x	x	x	x		6
A	x	x	x		x	x		5
J	x	x	x	x	x			5
G	x	x	x	x				4
D	x	x	x					3
I	x	x	x					3
C	x		x					2
F	x	x						2
Total Occurrences	10	9	9	5	5	4	2	

Table 2. Turnover rates between habitats within Nyack catchment. Higher values indicate greater turnover.

Habitat	Nyack creek lower floodplain	Nyack creek upper floodplain	Low elevation forests	High elevation forests	Alpine
Nyack floodplain	0.3	0.36	0.63	0.6	0.64
Nyack creek lower floodplain	X	0.16	0.5	0.55	0.63
Nyack creek upper floodplain	0.16	X	0.58	0.54	0.62
Low elevation forests	0.5	0.58	X	0.46	0.69
High elevation forests	0.55	0.54	0.46	X	0.79

Table 3. Overall contributions of endemic and overlap species to total richness by habitat and the catchment as a whole.

	Nyack floodplain	Low elevation forests	Alpine	Nyack creek upper floodplain	Nyack creek upper floodplain	High elevatoin forests	All habitats
Species richness	164	149	137	108	88	79	320
Endemic species	40	35	55	5	7	6	148
Overlap species	124	114	82	103	81	73	172
% Endemic species	24%	23%	40%	5%	8%	8%	46%
% Overlap species	76%	77%	60%	95%	92%	92%	54%

Table 4. Life form and dispersal analyses. A) showing percent species composition by life form for each habitat, and B) percent species composition by dispersal strategy for each habitat.

A.

Life form	Nyack floodplain	Low elevation forest	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests
Herb	65%	69%	79%	67%	61%	57%
graminoids	11%	6%	6%	7%	5%	4%
Shrubs	18%	19%	15%	19%	27%	27%
Trees	6%	6%	0%	6%	7%	12%

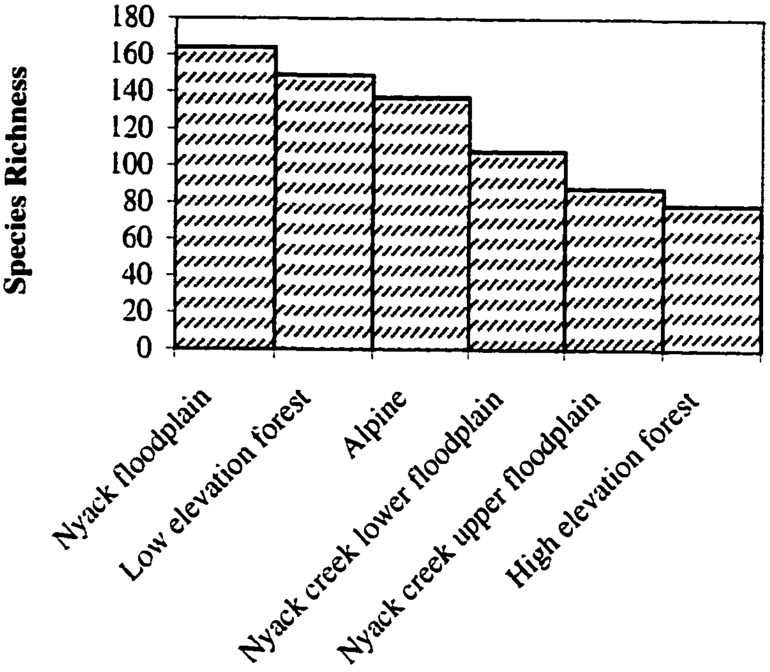
B.

Dispersal strategy	Nyack floodplain	Low elevation forests	Alpine	Nyack creek lower floodplain	Nyack creek upper floodplain	High elevation forests
Wind	51%	42%	47%	56%	51%	38%
Animal	16%	23%	11%	22%	24%	35%
Other	29%	33%	36%	20%	22%	22%

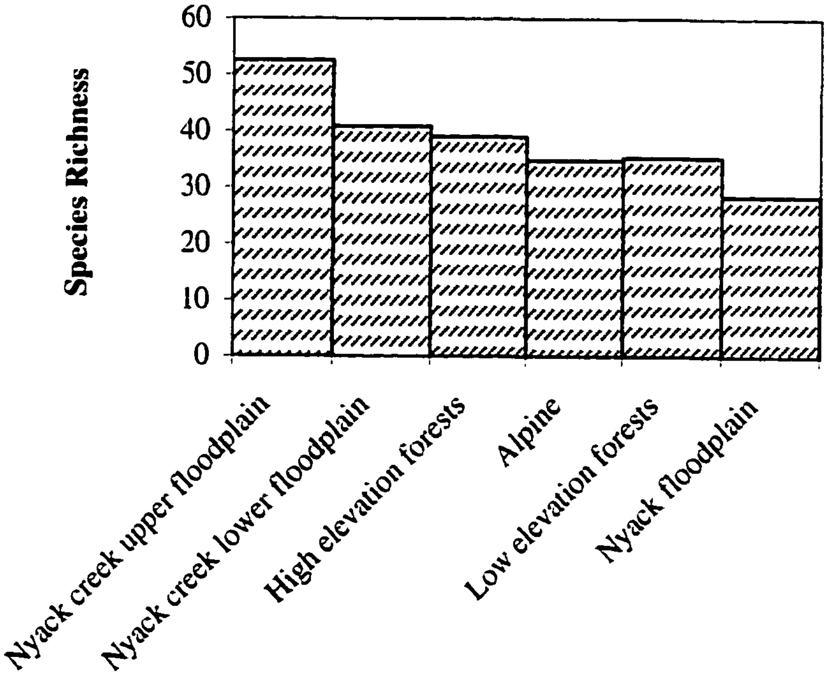
Figure 1. Species richness by physiognomic group. A) Catchment level patterns. B) Plot level patterns.

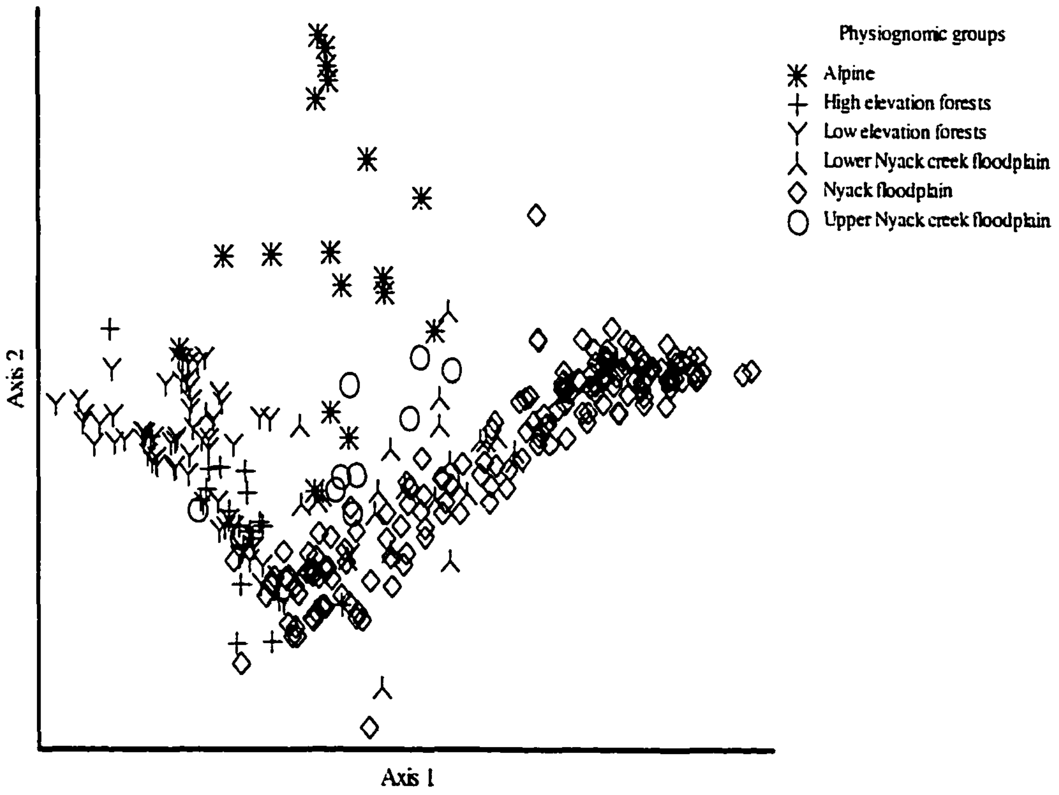
Figs. 2 (a-d): Ordination of plots based on species composition shows separation of habitats in multi-variate space (a), and the subplots (b-d) for species *Oplopanax horridum*, *Salix exigua*, and *Cornus stolonifera*, show where these species score highest on the DCA axes (indicated by symbol size).

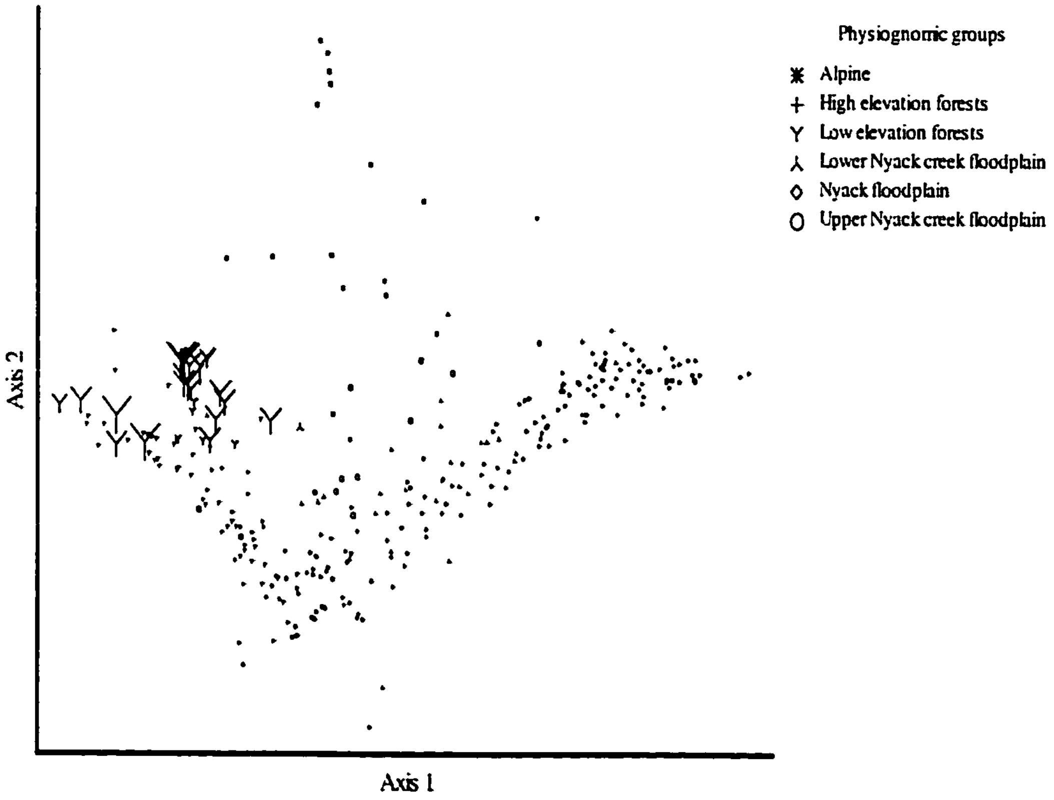
A

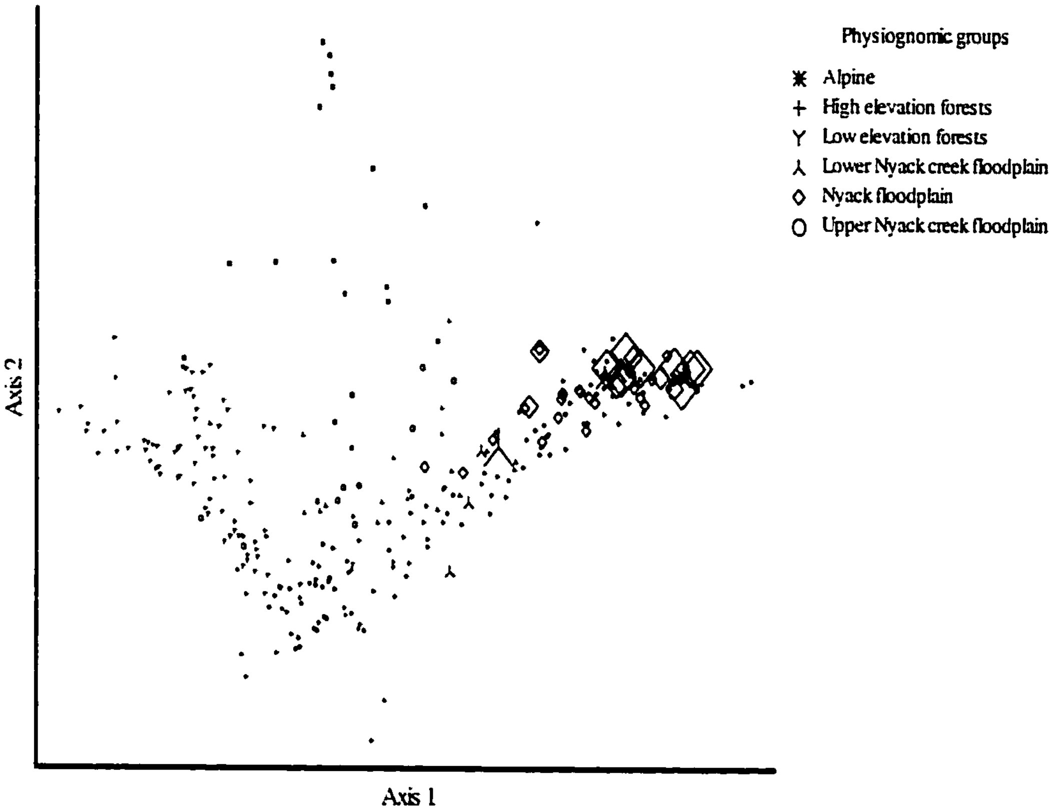

Species Richness
180
160
140
120
100
80
60
40
20
0
Nyack floodplain
Low elevation forest
Alpine
Nyack creek lower floodplain
Nyack creek upper floodplain
High elevation forest

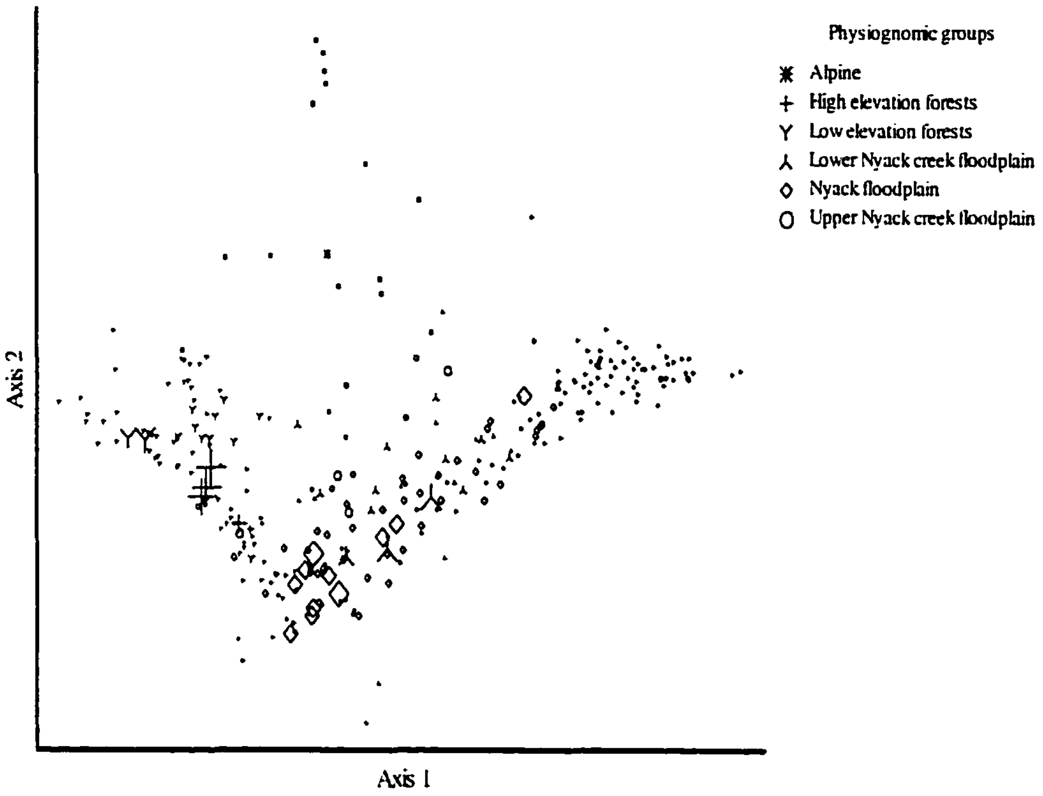
B


Species Richness
60
50
40
30
20
10
0
Nyack creek upper floodplain
Nyack creek lower floodplain
High elevation forests
Alpine
Low elevation forests
Nyack floodplain


Physiognomic groups
✳ Alpine
+ High elevation forests
Y Low elevation forests
⅄ Lower Nyack creek floodplain
◇ Nyack floodplain
○ Upper Nyack creek floodplain
Axis 2
Axis 1


Physiognomic groups
✱ Alpine
+ High elevation forests
Y Low elevation forests
⅄ Lower Nyack creek floodplain
◇ Nyack floodplain
○ Upper Nyack creek floodplain
Axis 2
Axis 1


Physiognomic groups
✱ Alpine
+ High elevation forests
Y Low elevation forests
⅄ Lower Nyack creek floodplain
◇ Nyack floodplain
○ Upper Nyack creek floodplain
Axis 2
Axis 1


Physiognomic groups
✱ Alpine
+ High elevation forests
Y Low elevation forests
⅄ Lower Nyack creek floodplain
◇ Nyack floodplain
O Upper Nyack creek floodplain
Axis 2
Axis 1

INFLUENCE OF FLUVIAL PROCESSES AND HYPORHEIC EXCHANGE ON FLOODPLAIN PLANT DIVERSITY AND PRODUCTIVITY.

Abstract. Flooding disturbance and associated fluvial processes operating on longitudinal and lateral floodplain axes are thought to control species richness patterns on floodplains in accordance with the Intermediate Disturbance Hypothesis. We expanded this idea to include riverine and groundwater (hyporheic) exchange operating on the vertical axis of large alluvial floodplains. Hyporheic exchange and fluvial processes create a shifting mosaic of wetland habitats that may substantially influence biotic patterns.

Vascular plant species richness gradients were not directly explained by flooding frequency for large flood plains on the Middle Fork Flathead river of Northwestern Montana, and the Talkeetna river of South Central Alaska. Rather, species richness on depositional point bars and forested benches was affected by hyporheic exchange at the floodplain scale and substratum fineness within reaches. Areas characterized by upwelling groundwater had the highest numbers of species (Flathead, $F = 11.6$, $p < .0001$, Talkeetna, $F = 4.8$, $p = .007$). On scour plains, richness was affected by percent cover of large wood debris (LWD) in plots ($r^2 = .656$, $p < .0001$) that interacts with flood flows reducing flow competence allowing for fine sediment deposition. Richness within regional upwelling and downwelling areas was highest at sites with the finest substratum (Flathead river, $r^2 = .501$, $p < .0001$, Talkeetna river, $r^2 = .810$, $p < .01$). Large floods deposit fine substrata in areas of low flow competence, which is not consistent with previous interpretations of the Intermediate Disturbance Hypothesis on river floodplains.

Radial growth rates of shrub and small tree species from the genera *Alnus* and *Salix*, used as indices of site productivity, were also significantly higher in scour plain and depositional bar habitats at areas characterized by upwelling on the Talkeetna river (*Alnus*, $F = 4.4$, $p = .027$, *Salix*, $F = 17.429$, $p = .0001$). Regressing *Alnus* and *Salix* growth rates against plot species richness showed positive, linear relationships ($r^2 = .76$, $p < .01$, $r^2 = .68$, $p < .01$).

These data show that patterns of species richness within these floodplains differ from those seen when single confined river reaches, or several wetland sites or river reaches are examined.

Key words: active alluvial floodplains, species richness, productivity, flooding disturbance, hyporheic exchange, substratum fineness, flood power.

Introduction

Floodplain habitats are rich centers of plant species diversity and productivity, perhaps the richest of all terrestrial habitats on earth (Naiman et al. 1993). These ecosystems are also critical centers of biological activity for diverse populations of amphibians, birds, and mammals (Kelsey and West 1998). It may seem intuitive that this high capacity for species packing is simply a function of flooding disturbances and their pervasiveness in space and time, whereby maximum species richness occurs at intermediate levels of flooding disturbance (Pollock et al. 1998). Many other ecological factors are involved in explaining floodplain species diversity, some of which have been little studied. These include regional species pools, and locally, groundwater – surface water exchange operating on the vertical dimension of floodplains.

Recently, studies have shown that floodplains have a tremendous ecological capacity to pack a relatively large proportion of the catchment species pool (Mouw and Alaback, in review, see figure 1). Studies have shown that regional species pools may be strongly influential in determining which and how many species are represented locally. Floodplains on the Middle Fork Flathead River, USA, and the Adour River in France are known to host 70% and 93% of upland species, respectively (Tabacchi 1992, Mouw and Alaback in review). It has been hypothesized that local floodplain plant assemblages are connected to regional species pools via the mechanistic linkages of water dispersal and associated catchment air flows (Naiman et al. 1993, Johansson et al. 1996, Andersson et al. 2001, Mouw and Alaback in review).

This tremendous ecological capacity for relatively high species richness is thought to arise from the heterogonous character of unconfined alluvial floodplains in space and time. A mosaic of habitats resulting from fluvial processes leads to a wide variety of unique geomorphic surfaces per unit area that consequently result in high species turnover between habitats. Large, braided alluvial floodplains characterized by frequent channel migration in response to cut and fill alluviation are known to be the most dynamic in space and time. These diverse habitat mosaics shift or change in time to produce a wide variety of plant species and communities as well as successional diversity within these communities due to the instability of channel matrices composed of fluvially derived materials (Stanford and Naiman in press). These factors and processes make these features of lotic systems unique in structure and function from confined or stable rivers or river reaches that do not migrate laterally on such a frequent basis, if at all.

On alluvial flood plains, ecological structure varies along the longitudinal river axis in response to the relative roles of erosional and depositional processes. Erosional processes dominate headwaters while depositional processes become more important downstream and are greatest at river deltas. Montane floodplains are considered in transitional zones where erosional and depositional processes operate in concert to produce the greatest spatial heterogeneity in substratum structures and relatively intermediate disturbance regimes within a catchment context. As montane floodplains are typically the richest in plant and animal species (Tabacchi et al. 1998, Ward 1998), the Intermediate Disturbance Hypothesis is upheld (Ward and Stanford 1983). In addition, studies accounting for entire longitudinal river continua have shown that richness is greatest on floodplain sites with the greatest substratum heterogeneity, and intermediate substratum fineness (Nilsson et al. 1989).

In more confined, and therefore physically stable rivers or reaches of specific rivers, sites flooded on an intermediate basis are generally the richest in plant species, giving the impression that species richness is simply a function of disturbance frequency on unconfined floodplain landscapes, and that the predictions of the Intermediate Disturbance Hypothesis are not scale dependent. This interpretation suggests that local richness should be greatest at sites with the greatest substratum heterogeneity and intermediate substratum fineness as these sites should be intermediately disturbed (Tabacchi et al. 1998). This is true because sediment transport competency is directly related to flood power, or disturbance intensity.

Another key tenant of community ecology is that community richness is also a function of site productivity, where maximal richness generally occurs at sites of intermediate productivity. Pollock et al. (1998), using plant richness data from a variety of wetland types supported the Intermediate Disturbance Hypothesis as it relates to Huston's (1994) Dynamic Equilibrium model: high diversity sites were subject to intermediate flood disturbance frequencies. These ideas have not been examined within a single, well-defined flood plain of the middle reaches of a gravel-bed river where diversity should be high. The prediction is that richness is also a function of site productivity within a single floodplain with the caveat that physical factors that determine site productivity are not clearly understood.

While flooding and associated fluvial processes are indeed highly influential in determining species richness of floodplains, and perhaps gradients of species richness within floodplains, plant ecologists have yet to account for the four-dimensional nature of lotic ecosystems (sensu Ward 1989). Subsurface hydrogeologic patterns and processes recognized by stream ecologists and hydrogeologists for decades; namely linkages between alluvial groundwater and stream water, or groundwater – surface water interaction (GW-SW) are known to strongly influence the ecology of floodplain landscapes (Stanford and Ward 1993, Naiman et al. 2000). Alluvial floodplains are unique hydrogeomorphic features of catchments where streamflows are routed through complex channel matrices and porous substrata; leading to groundwater - surface water exchange and a variety of subsequent hydrologic conditions at several scales. Hyporheic zones are those characterized by the mixing of surface and groundwater, ultimately the linkage between surface and subsurface hydrologic conditions (Stanford and Ward 1993). The nature of hyporheic zones is largely controlled by floodplain geomorphology, where geomorphically controlled flux rates of groundwater through floodplain substrata lead to transient storage of infiltrating river water. In fact, many large floodplains of the west have a tremendous capacity for transient storage of water within subsurface interstices, where models have shown the volume of water in transient storage (relative to surface water) to range from 3 - 460 % (D'Angelo et al. 1994).

While hyporheic zones are considered to have profound impact on the ecology of river environments, plant scientists have rarely examined river-groundwater exchange as a driver of local environmental controls that may strongly affect species richness. Studies have shown that woody plants have higher interspecific growth rates at sites underlain by alluvial aquifers (see Stromberg 1993, Rood et al. 2000). Also, Harner and Stanford (in review) documented higher growth rates in upwelling areas of a flood plain. However, studies investigating the affect of hyporheic exchange on plant species richness appear to be lacking.

We examine herein plant species richness and site productivity within a single floodplain reach of a Rocky Mountain River and a coastal river in Alaska. We show that in both cases species richness and productivity are highest in the upwelling areas (floodplain scale) and influenced at the site (habitat unit) scale by flooding and sedimentation, but in ways that are inconsistent with the Intermediate Disturbance Hypothesis.

Methods

Study Sites

Large alluvial floodplain reaches of the Flathead River, Montana, and the Talkeetna River, Alaska, were used as study sites. The Nyack floodplain of the Middle Flathead River is the southern boundary of Glacier National Park. This river system was selected as it is relatively pristine and has been the focal point of studies in floodplain ecology and hyporheic exchange in recent years (Stanford and Ward 1988, Malanson and Butler 1990, Stanford and Ward 1993, Stanford et al. 1994, Wissmar et al. 1997, Pepin and Hauer in review, Harner and Stanford in review, Poole et al. 2001 in review). The Middle Fork has a snow - dominated hydrograph with peak flows typically in June during peak snow melt. The Nyack floodplain is approximately 9 km long and up to 3km wide, and is characterized by one primary channel, though during high flows many secondary, back-bar, and spring brook channels receive flow. Mean annual flow of the Middle Fork, determined by US Geological Survey (USGS) gauging station (#12358500) is 82 m^3/s (cms), with base flows averaging 17 cms and peak annual discharge averaging 541 cms. Floodplain vegetation is dominated by several age classes of *Populus balsamifera* Hitchcock., and shrub communities characterized by *Salix* species and *Alnus incana* Hitchcock. on surfaces flooded on a relatively frequent basis. Forests fringing the floodplain are dominated by cottonwood *Populus balsamifera* and Engelmann spruce (*Picea engelmanii*) tree species, with Douglas fir (*Pseudotsuga menziesii*) and subalpine fir (*Abies lasiocarpa*) also present in many stands. Sampling of this floodplain was focused on a 2 km reach where a sharp gradient from downwelling to upwelling occurs.

The Talkeetna River has a glacially dominated hydrograph and is a tributary of the Susitna River of South Central Alaska. It originates in glacial terrain of the Talkeetna Mountains and flows primarily to the west through unconfined floodplain reaches and one bedrock-confined canyon. Sampling of vegetation occurred along a floodplain reach beginning at USGS gauging station (# 12497001) and extending 11 km downstream to the village of Talkeetna and confluence with the Susitna River. Multiple primary channels characterize this reach; with many secondary, backbar, and spring brook channels becoming active at high flows. Some spring brook channels remain flowing all year long and can be found up to 50 m from the edge of the active floodplain. Mean annual flow of the Talkeetna River is 127 cms, with peak annual discharge averaging 832 cms as determined from 36 years of record from the USGS gauging station. Floodplains of the lower Talkeetna River are characterized by *Alnus* *incana* Hulten., and *Salix bebbiana* Hulten. shrub communities on the active floodplain, with *Populus balsamifera* Hulten. – *Picea glauca* forests fringing the floodplain.

Habitat descriptions

Three broad habitat classes were designated. Both the Flathead and Talkeetna Rivers share similar species dominance patterns with the dominant cover types being *Salix* and *Alnus* shrub communities and *Populus* forests. Fringing each of the floodplains is mixed *Populus – Picea* forests on relatively high *flood plain benches* that are infrequently flooded. Sites lowest in elevation are frequently within the parafluvial zone that is annually flood-scoured and are called *scour plains*, though these habitats are found at a variety of elevations. Scour plain habitats are typically dominated by gravel and larger material as fine sediments have been eroded from the surface. Plant colonization is restricted by unsuitable substratum and intense disturbance, and as a result few species colonize these habitats and total plant cover is relatively low. *Depositional habitats* occurred where stream power is reduced during floods allowing deposition of fine sediments. On the Flathead River, depositional habitats show a mixed composition of *Salix*, *Alnus* and *Cornus* shrub species, while *Alnus incana* dominates depositional sites on the Talkeetna River.

Sampling Protocol

Within selected floodplains, transects were placed perpendicular to primary river channels and extended across the entire width of the floodplain. Four transects were sampled on both the Middle Fork Flathead and Talkeetna rivers. Specific locations of these transects was further determined by channel characteristics allowing for suitable surface water hydrography measurements (see Rantz et al. 1982). Along each transect, 2 x 50 m (100 m^2) plots were placed at 50-meter intervals, with the first plot beginning at the edge of the river channel (after Gentry 1982). Each plot was divided into five 10 x 2m segments where environmental variables, and species presence-absence, and percent cover were recorded for all species.

For shrub and tree species, basal diameters, height, and age were also recorded to allow for the determination of growth rates. Basal diameters were determined by measuring stem cross-sections, or with a calibrated diameter tape for larger shrubs and trees. Plant height was determined by actual measurement of those cut, and a clinometer for larger, taller plants. Age was determined by counting radial growth rings from stem cross-sections or with an increment borer, used to extract cores at the base of stems. Growth rate was determined by dividing stem diameter by plant age, and was used as an index of site productivity.

Within each plot segment the environmental variables substratum fineness, depth of surface substratum, percent cover of LWD, and relative elevation was recorded. Substratum fineness was determined by hand texturing using a detailed soil key of fourteen soil textures ranging from cobbles to clay (after Thien and Graveel 1997). The elevations of plots relative to the nearest river channel were measured with an auto level and stadia rod, where accuracy was +/- .05 cm.

For each transect, surface and subsurface hydrologic conditions were monitored throughout the entire field season, from May – August. At each channel cross-section, river stage was monitored from established benchmarks. River stage was determined with an auto level and stadia rod. The relative elevation of each plot was also determined from the same benchmark allowing for the quantification of flooding frequency for each plot once a stage-discharge relationship was established for each cross-section (discussed subsequently).

Along each transect, a minimum of five piezometers were also installed on each side of the river and extending away from the channel until floodplain surface elevations became greater than 1.5 m above the river channel. Stage recordings were taken within each piezometer on each day river stage was measured. Stages within piezometers relative to surface water stages were determined with an autolevel and stadia rod.

Analysis of Floodplain Hydrology

Relative stage readings of river stage and corresponding stages within piezometers were analyzed for head differences. Sites where GW stage is greater than SW stage indicated a positive VHG, and upwelling, while the opposite was true for downwelling. Corresponding GW and SW stage readings for each cross section were entered into a spreadsheet allowing for the construction of line graphs used to assess the GW-SW connectivity within each river system and at each floodplain cross section.

Stage-discharge curves were developed for each cross section by regressing stage observations against discharge measurements at an upstream USGS gage on the Talkeetna River, and an upstream data logger on the Flathead River. Using this relationship in conjunction with each river's flow duration curve allows for the prediction of flooding frequency at a given river stage. We determined flooding frequency as the number of times a plot is inundated per year (after Pollock et al. 1998). Once the relative elevations of plots at each cross section was quantified, plot flooding frequency was determined based on the period of record, which was 61 and 36 years on the Flathead and Talkeetna rivers, respectively.

Data Analyses

Species and environmental data were entered into spreadsheet matrices and proofread for accuracy in transcription. To explore initial patterns in each species matrix ordinations of sampling plots were performed with Detrended Correspondence Analysis (DCA) using 26 segments in detrending. Specifically, this ordination technique was used to ordinate plots from different habitats in species space, allowing for the interpretation of variables influential in the ordinations, and to determine if species distribution and abundance patterns differ amongst the *a priori* habitat types. DCA is also useful in determining beta diversity (species turnover) between plots as the distances between points directly reflect differences in species composition.

Univariate explorations were then employed to investigate hypotheses derived from the ordinations. Correlation analysis was used to search for environmental variables that relate to species richness, and regression was used to model relationships. Specifically, we used these analyses to test for predicted relationships developed from the literature between flooding frequency, substratum fineness, substratum heterogeneity, and species richness. These approaches were also used to investigate influences of LWD on plot species richness. Differences in species richness and productivity between sites of contrasting GW-SW interaction were analyzed by analyses of variance (ANOVA), as floodplain reaches were classified as either (1), neutral VHG, (2) downwelling, or (3) upwelling. One-way ANOVA with species growth rates as the dependent variables and VHG as the categorical variable were conducted. Two-way ANOVA, including both VHG and habitat type as fixed factors, were conducted to determine if VHG explains differences in species richness within habitat types. Prior to analyzing the species data, the plot species richness data were log transformed to satisfy the homogeneity of variances assumption of ANOVA.

Results

Floodplain Hydrology

In both systems gradients in subsurface hydrology were identified. On the Flathead River a strong gradient from downwelling to upwelling was identified along a short 2 km segment of the Nyack floodplain, which also was the widest floodplain segmement. The upstream end of this segment shows strong downwelling patterns, where the water table was .5 m below river stage near the main channel and up to a meter below river stage at the edges of the active floodplain. The downstream portions of this segment showed the opposite pattern. Near the primary river channel ground water head was always greater than river stage, often by 3 cm or more. Further, GW-SW connectivity was strong, as stage fluctuations within all piezometers reflected the instream hydrograph (figure 2). These patterns mirrored results of a previous study (Stanford et al., in review) that demonstrated regional water influx and efflux from mass balance measures.

Gradients in subsurface hydrology were also observed on the Talkeetna River. The upper-most transect was characterized by upwelling, where groundwater stage was 6 cm higher than river stage near the main channel throughout the entire field season. Below this section the river begins to downwell and loses instream flow to the floodplain aquifer that was seen to be 10cm lower than river stage. The remaining two downstream transects were found to have a neutral VHG. GW-SW connectivity was also strong in this system, though aquifer stages were not as responsive to surface water fluctuations. This is likely due to the lower hydraulic conductivity of the fine glacial sediments that dominate much of the floodplain. In fact, some sites dominated by silt had what appeared to be a perched water table. As these sediments were saturated during flooding they retained water well after groundwater stage declined (as shown by neighboring piezometers), leaving saturated conditions in these sediments of low conductivity.

Relationships to Surface Hydrology

Ordinations of the species data showed distinct groupings of plots into *a priori* habitat categories based on physical environmental factors (figures 3a and 3b). The first axis on both DCA scatter plots shows similar patterns, where plots scoring at the extremes of these axes are scour plain plots and gallery forest plots, while depositional habitats are found in the central portions of the first axes. These first axes suggest that flooding frequency may drive patterns in vegetation on the lateral river axis, as we expected scour plains to be frequently flooded, depositional bars flooded at an intermediate frequency, and forested benches to be infrequently flooded. However, when each of the first axes is regressed against flooding frequency, no relationship is apparent. As these results are puzzling and contradict the well-established idea that plant species and community types are aligned on elevational gradients on floodplains, relationships between plot species richness and habitat type were also explored. Again, the data show that flooding frequency cannot be used as a predictor of habitat (figure 4a) or plot richness (figure 4b) with these data.

Maximal richness on the Flathead and Talkeetna Rivers was found at different sites. On the Flathead River, richness peaked at 70 species within *Populus-Picea* bench plots that had the highest average plot richness of all floodplain surfaces (51 species/100 m^2). On the Talkeetna, the greatest richness occurred within *Alnus* dominated depositional bars where richness was as high as 40 species and averaged 38 species/100 m^2. These depositional as well as scoured surfaces were not found at a consistent elevation (figure 5) and were flooded at a wide range of frequencies, indicating again, that frequency of flooding disturbance cannot be used to predict species richness.

Relationships to Subsurface Hydrology

Comparing richness levels within habitats and between sites of contrasting GW-SW interaction shows significant differences on both river systems (figures 6a and 6b). Analysis of variance showed that plot richness is significantly greater at upwelling sites than downwelling sites when plots from all habitats are considered on the Flathead River (Table 1). Further investigation of these differences in species richness, however, shows that a significant difference does not exits between scour plain sites on this system, suggesting that other factors are more influential in controlling species richness at these primary stages of plant succession. Testing for differences in species richness on the Talkeetna River shows similar trends, as significant differences are seen in average plot richness between upwelling, and downwelling transects, but again only within terrace and depositional habitats (Table 2 and 3). Scour plains did not occur at every floodplain transect on the Talkeetna River, and were excluded from this analysis.

Growth rates of the species *Alnus incana*, *Salix bebbsiana*, and *Salix alexensis* showed similar responses to VHG (Figure 7). All of these species showed significantly higher growth rates at depositional bar sites characterized by upwelling groundwater than at sites characterized by downwelling (Table 4). Further, using the growth rates of these species as indices of site productivity results in a significant positive correlation between plot species richness and productivity (Figure 8).

Influence of Sediment Structures

Entire data sets from both rivers show a positive and significant correlation between plot richness and substratum fineness (figures 9a and 9b). This relationship remains consistent within transects as well, indicating that substratum fineness explains, in part, residual variation in species richness within a floodplain reach. In fact, on scour plains of the Flathead River, where deposition of fine substrata is influenced by LWD, species richness is positively related to the percent cover of LWD within plots (figure 10). This suggests that LWD is the primary driver of species richness gradients on scour plains of this river, as VHG has no influence with these data. Relationships between substratum heterogeneity and species richness were not found with these data.

Discussion

The data show vertical hydraulic gradient is the primary predictor of vascular plant species richness between comparable sites within floodplains. Further, growth rates of overstory plants positively relates to site richness, showing that VHG may also be used as a predictor of site productivity. As this gradient in subsurface hydrology is a naturally occurring phenomenon on the longitudinal axis of many alluvial floodplains, three hypotheses are suggested to explain gradients in species richness and productivity that were found to respond to VHG. As upwelling river reaches are likely buffered against annual reductions in streamflow, richness and productivity gradients may simply be explained by water availability. Whereas aquifer levels at downwelling river reaches are solely dependent upon river stage, upwelling sites may be dependent, in part, on hillslope water sources. Even if upwelling is solely a product of subsurface geology, reductions in aquifer stage should be less relative to downwelling reaches during river stage decline. A second plausible hypothesis rests on the thermal and chemical differences between upwelling and downwelling groundwater. As downwelling reaches are characterized by groundwater that is thermally and chemically similar to surface water, upwelling sites are often rich in N and dissolved C (Ford and Naiman 1989), nutrients which are available to plants during the growing season when river stage is high (Bansak 1998). As N may be limiting on floodplains, plants at upwelling sites may meet their nutritive needs at a lower cost, which may explain increased growth rates at these sites. Further, increased nutrient availability may provide for more niches in space and time to provide for the relatively high levels of species coexistence at these sites. Lastly, because upwelling sites are thermally buffered, plants at these sites may become or remain biochemically active earlier in spring and later in summer relative to plants at downwelling sites.

Flooding as a factor

Although flooding and associated fluvial processes largely control floodplain structure, and make these ecosystems richer in species than other terrestrial habitats, the frequency in which a site is flooded is a poor predictor of species richness within unstable alluvial floodplains. The current analysis shows that when flooding disturbance is measured by frequency, the Intermediate Disturbance Hypothesis is not upheld within these floodplain units. Studies on floodplains have also shown that coupling intermediate disturbance with intermediate levels of productivity explains maximal richness on floodplains supporting the Dynamic Equilibrium Model of Huston (1979). These data do not conform to these general patterns, as species richness was seen to increase in a linear fashion with site productivity. These data are reported in the present paper to note that the data provide an interesting exception to these widely cited and empirically supported hypotheses, not to question them in general. It does appear however, that species richness is a product of intermediate disturbance only at catchment scales, as originally discussed by Ward and Stanford (1983).

When we consider the residual variation in site species richness explained by substratum fineness, and to some degree, substratum depth, the above relationships with flooding frequency are better understood. In many cases, two sites compared in this analysis reveal the same flooding frequency and duration, however patterns in sedimentation on these plots shows that one site has been soured, while the other filled. As scouring often erodes surfaces to expose cobbles and gravels, filling processes deposit finer sediments. Because channel complexity is great on many alluvial floodplains, spatial variation in flood power is often great (Bendix 1999), resulting in dynamic mosaics of scour and fill sites differing in hydrology and geomorphology, making patterns in sedimentation a better predictor of species richness than flooding frequency, as this factor represents disturbance intensity. However, even when considering flood power rather than flood frequency, the Intermediate Disturbance Hypothesis is not supported at the floodplain scale, as sites with the greatest substratum fineness are richest in species. These conditions reflect low flow competence and relatively low disturbance intensity.

Patterns in Sedimentation

Though fluvial processes are largely controlled by the capacity of a given river reach to do geomorphic work (which relies on channel slope and water depth), patterns in sedimentation are somewhat predictable. General patterns in sedimentation are seen between the Flathead and Talkeetna rivers. On large geomorphic surfaces, such as floodplain islands, and obvious scour – fill gradient can be observed on the longitudinal island axis. Typically, upstream island segments are scoured free of finer sediments, as larger materials are deposited or exposed. Working downstream, finer sediments develop and thicken, and become the finest and deepest at the downstream segments of islands where depositional point bars form. This pattern in sedimentation represents a gradient in stream power, which is greatly diminished at confluences of back-bar or secondary channels with primary channels creating backflow in lesser channels. This reduction in stream power precipitates the deposition of fine substrata that provides for point bar accretion. Patterns in species diversity reflect these gradients in stream power showing that regardless of river reach (i.e. upwelling v. downwelling); species richness is highest at sites with the finest substrata, which again indicates that richness gradients at a particular floodplain position are largely controlled by substratum fineness, while variation in species richness between floodplain reaches is largely controlled by GW-SW interaction.

At smaller scales, (e.g. within a geomorphic feature) LWD transport and deposition to floodplain surfaces during flood events also influences patterns in sedimentation and species assemblage patterns (Malanson and Butler 1990). At points of deposition, LWD acts as a local barrier that reduces stream power and leads to the deposition of fine sediment lenses immediately downstream, where size of such lenses is directly proportional to LWD complex size. Indeed the data show that percent cover of LWD largely influences species richness within the scour plains of the Flathead River. This influence is especially pronounced on the Flathead River that has a much lower sediment load relative to the glacially influenced Talkeetna River, even during peak flows. As the Talkeetna carries a tremendous sediment load, LWD is likely less influential. Even so, intensively scoured surfaces show vegetation development restricted to sediment lenses associated with LWD on this system (personal observation). Leaving scour plains, LWD becomes less influential as patterns in sedimentation are driven by larger scale factors and processes. In fact, the data from the Flathead River show that LWD is the primary factor influencing species richness on scour plains, while within depositional bars and surfaces further along the successional pathway are primarily influenced by subsurface hydrology.

Conclusions

The data show that an understanding of plant species richness and productivity patterns within alluvial floodplains requires the inclusion of vertical river dimensions. Gradients in interstitial hyporheic flow not only affect instream and hyporheic animal communities, but also terrestrial plant communities. Though patterns in sedimentation greatly influence plant community dynamics, GW-SW interaction appears to be the dominant predictor of the species richness of floodplain plant communities and productivity of constituent taxa on both rivers. Explanation of residual variation in species richness by substratum fineness reveals that flood power, not flooding frequency influences species richness patterns, and without exception, sites flooded the least intensively are the richest in species. As these results were consistent on both river systems, they apparently are not regional phenomenon. Further studies are needed to investigate these patterns on an experimental basis to better understand, in terms of plant physiology, what factors are driving patterns in species richness and productivity on alluvial flood plains.

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Table 1. Analysis of variance in species richness explained by factors VHG, and Habitat.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	4143.444	5	828.689	11.646	.000
Intercept	24072.364	1	24072.364	338.303	.000
VHG	836.364	1	836.364	11.754	.002
HABITAT	3238.179	2	1619.090	22.754	.000
VHG * HABITAT	452.779	2	226.390	3.182	.056
Error	2063.528	29	71.156		
Total	33591.000	35			
Corrected Total	6206.971	34			

R Squared = .668 (Adjusted R Squared = .610)

Table 2. Analysis of variance in species richness on the Talkeetna River explained by factors VHG, and Habitat.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1119.869	7	159.981	4.824	.007
Intercept	7404.259	1	7404.259	223.287	.000
VHG	219.979	2	109.989	3.317	.069
HABITAT	583.640	2	291.820	8.800	.004
VHG * HABITAT	332.145	3	110.715	3.339	.053
Error	431.083	13	33.160		
Total	11671.000	21			
Corrected Total	1550.952	20			

R Squared = .722 (Adjusted R Squared = .572)

Table 3. Analysis of variance in species richness on the Talkeetna River excluding scour plain habitats.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	803.021	5	160.604	3.880	.032
Intercept	6632.414	1	6632.414	160.235	.000
VHG	388.783	2	194.392	4.696	.036
HABITAT	240.120	1	240.120	5.801	.037
VHG * HABITAT	44.415	2	22.208	.537	.601
Error	413.917	10	41.392		
Total	10481.000	16			
Corrected Total	1216.938	15			

R Squared = .660 (Adjusted R Squared = .490)

Table 4. One-way Analysis of Variance in growth rates of *Alnus* and *Salix* by floodplain position.

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups *Alnus*	342.5	2	171.3	4.430	.027
Within Groups *Alnus*	695.8	18	3865		
Total *Alnus*	.104	20			
Between Groups *Salix*	.126	2	627.8	17.429	.0001
Within Groups *Salix*	468.3	13	3602		
Total *Salix*	.172	15			

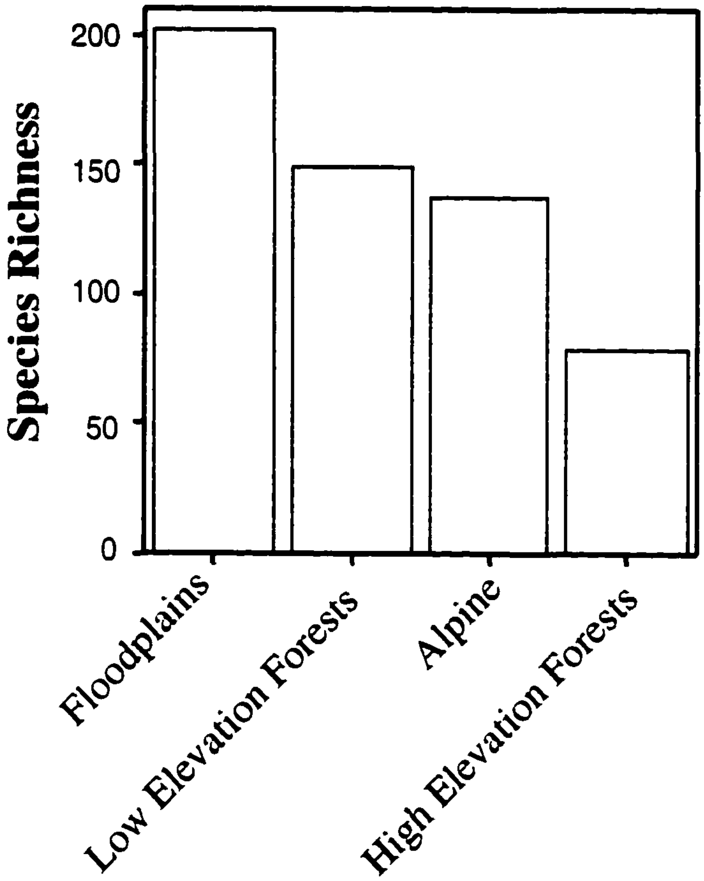


Figure 1. Species richness by ecosystem types sampled on the Middle Fork Flathead Catchment (adapted from Chapter 1).

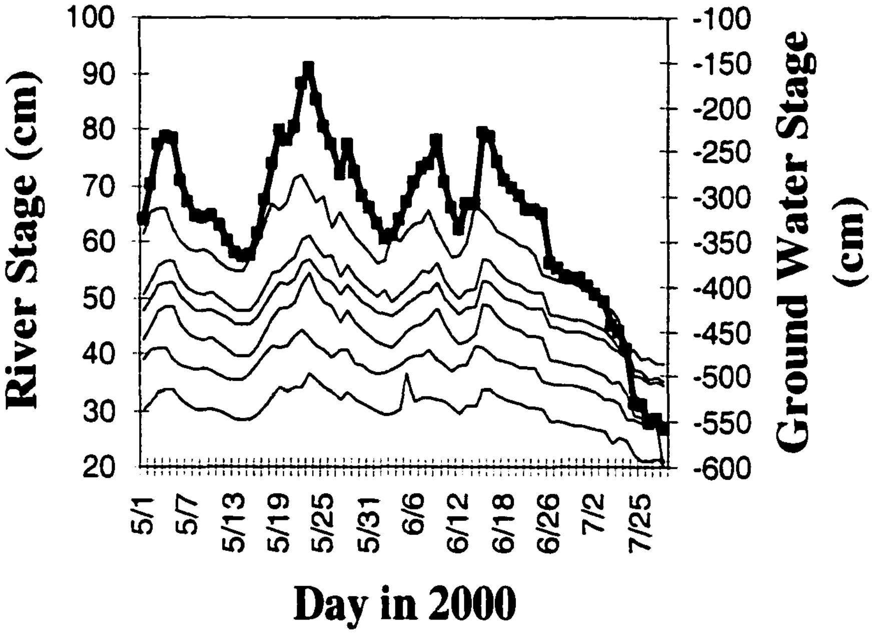


Figure 2. Line graph showing connectivity between groundwater and surface water (dark line). Stages are not relative to one another.

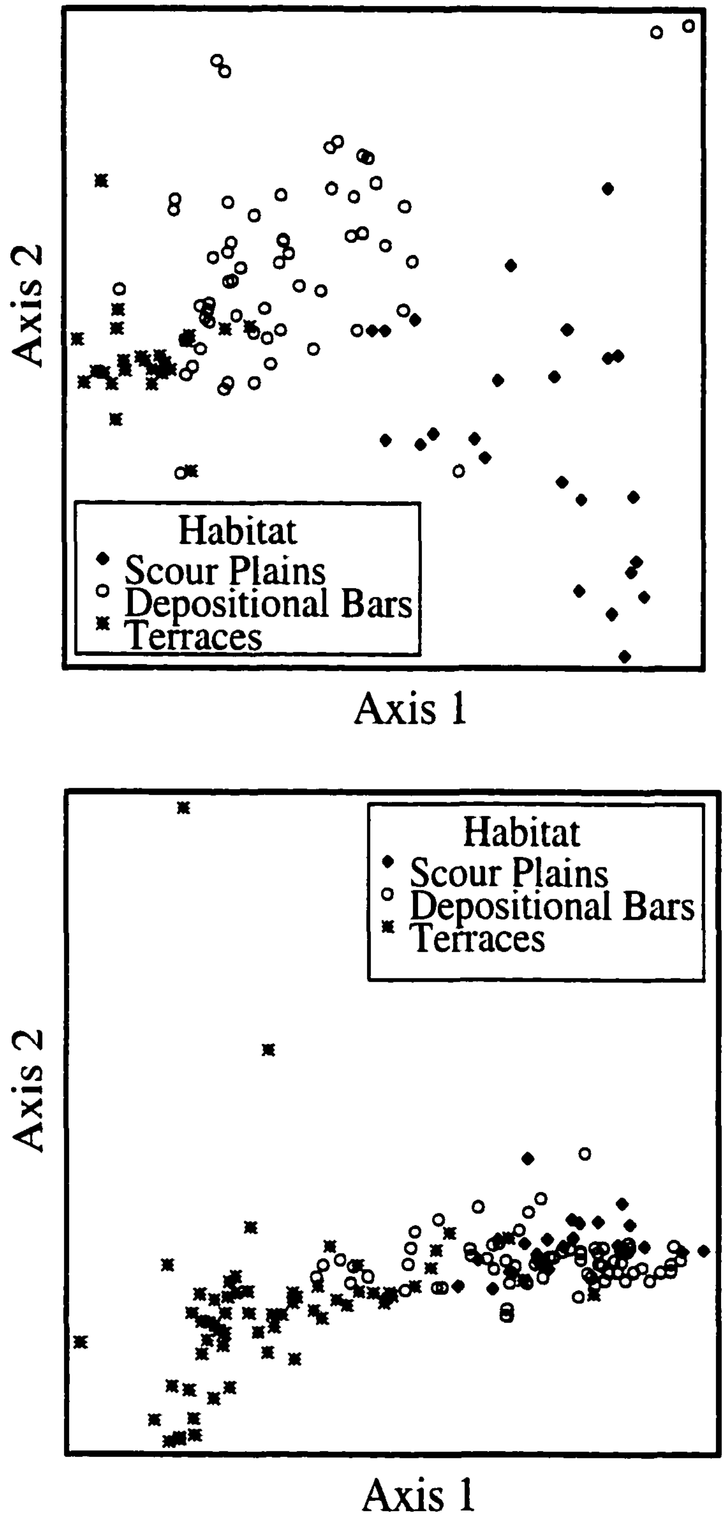


Figure 3. DCA scatterplots of first two axes, showing separation of plots based on species composition in multivariate space on (a) Talkeetna River, (b) Flathead River.

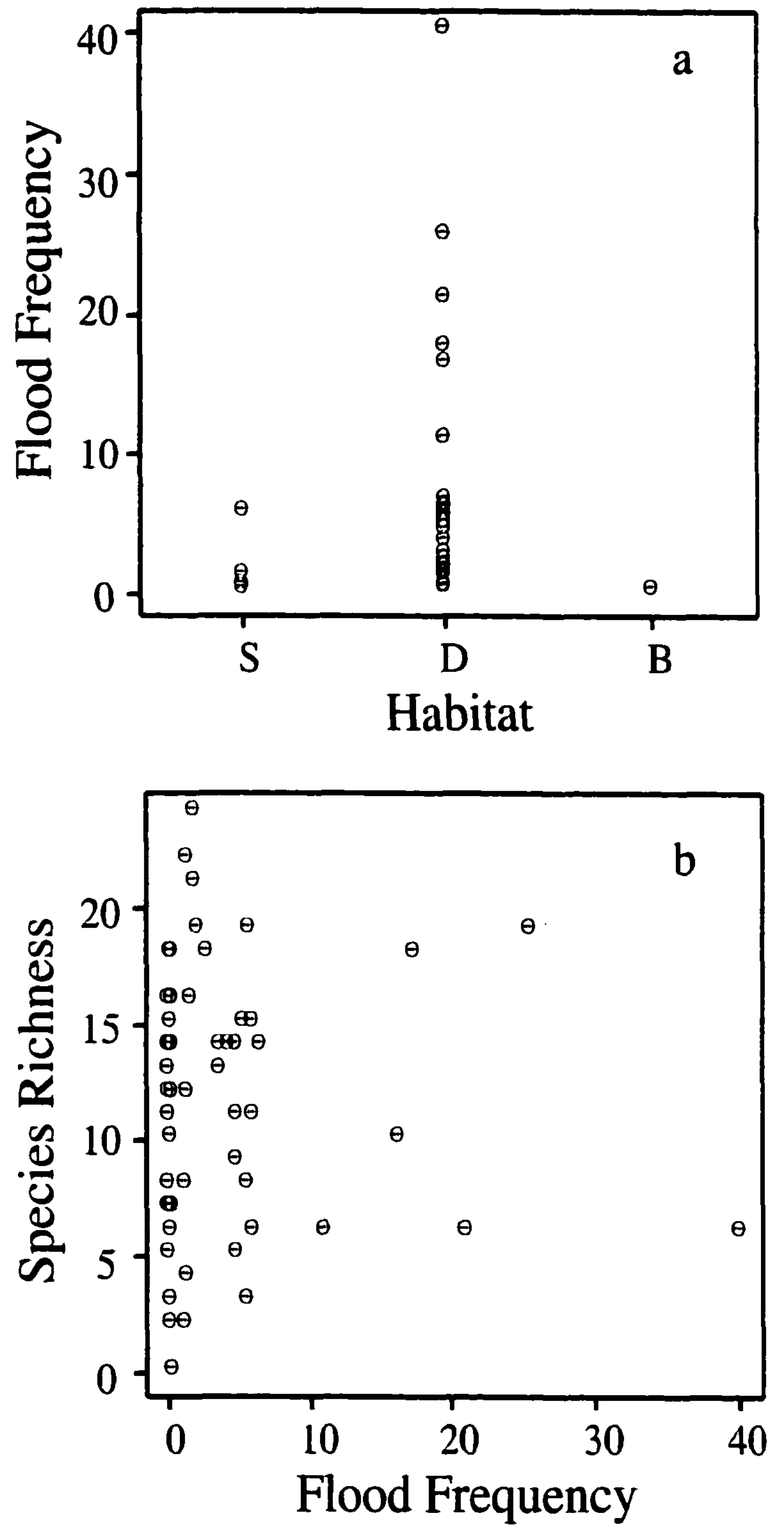


Figure 4. (a) Habitats (S = Scour plains, D = Depositional Bars, and B = Forested Bench) on Talkeetna River vs. their flooding frequency, (b) plot species richness vs. flooding frequency (# of times flooded per year).

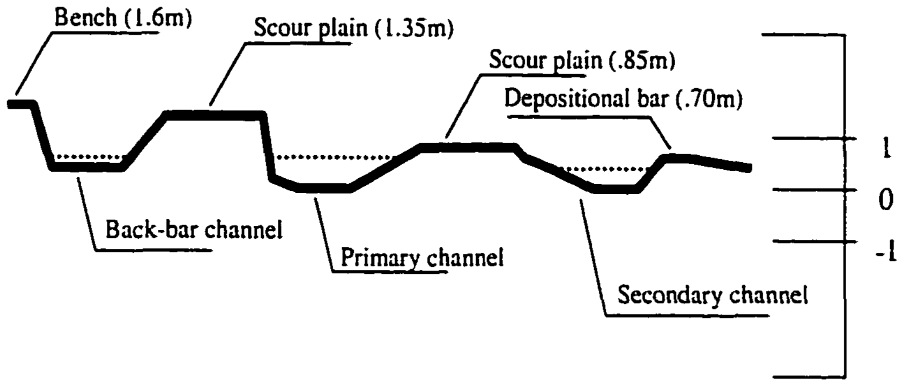


Figure 5. A cross section on the Talkeetna River, Alaska, illustrating actual elevational profile of habitats and channel types present. Note the inconsistent vertical positioning of habitats. Lateral distances are not to scale.

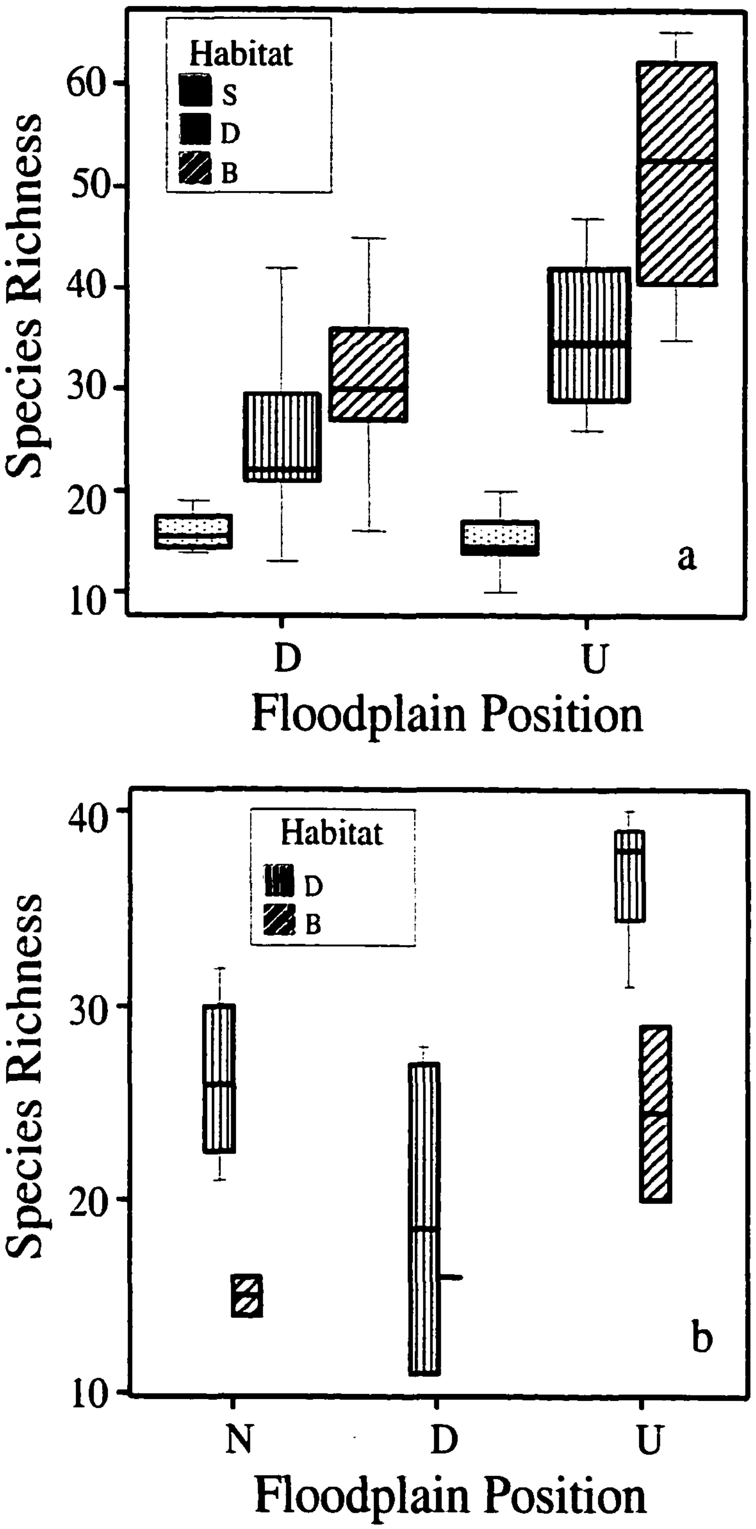
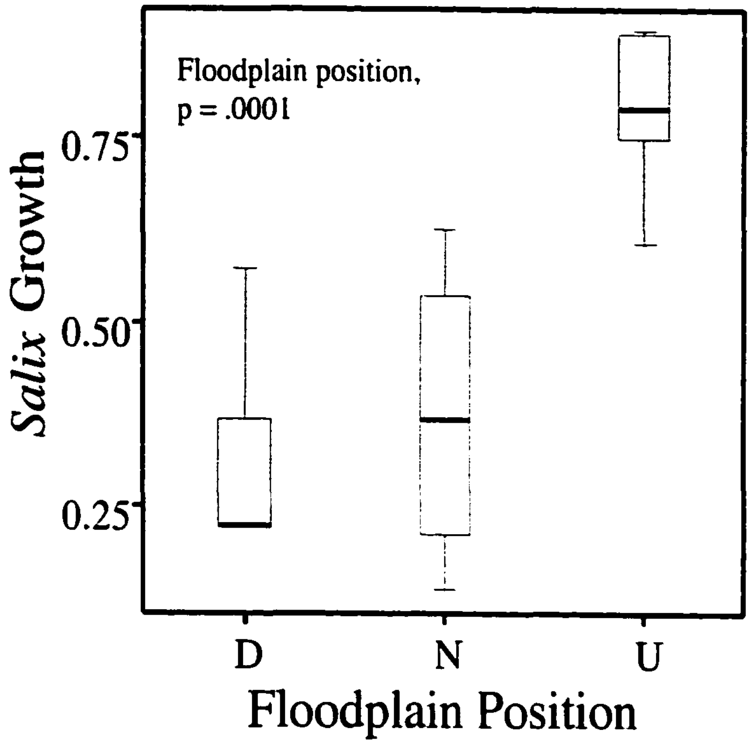


Figure 6. Species richness by floodplain position on (a) Flathead River, (b) Talkeetna River (N = neutral, D = downwelling, U = upwelling).



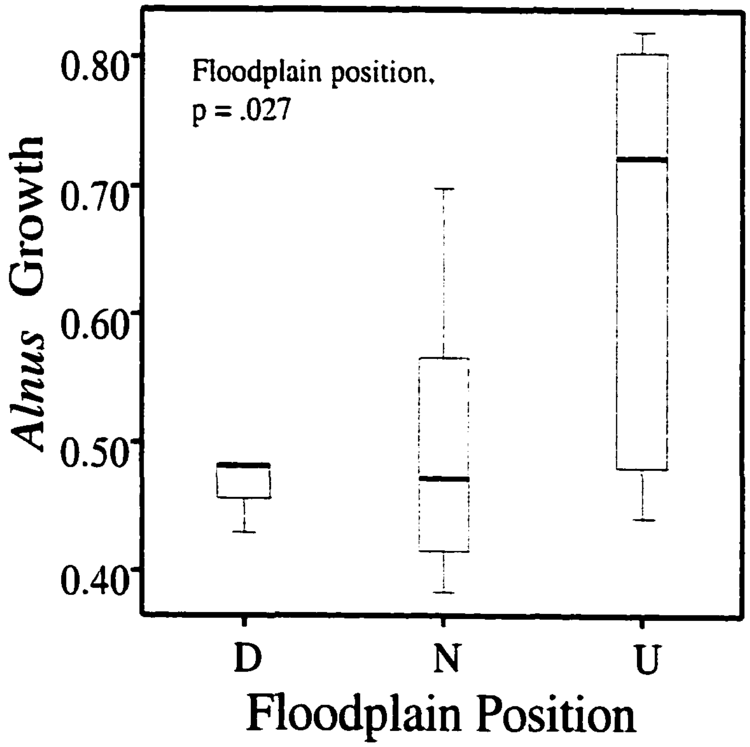


Figure 7. Growth rate by floodplain position on the Talkeetna River. (N = neutral, D = downwelling, U = upwelling).

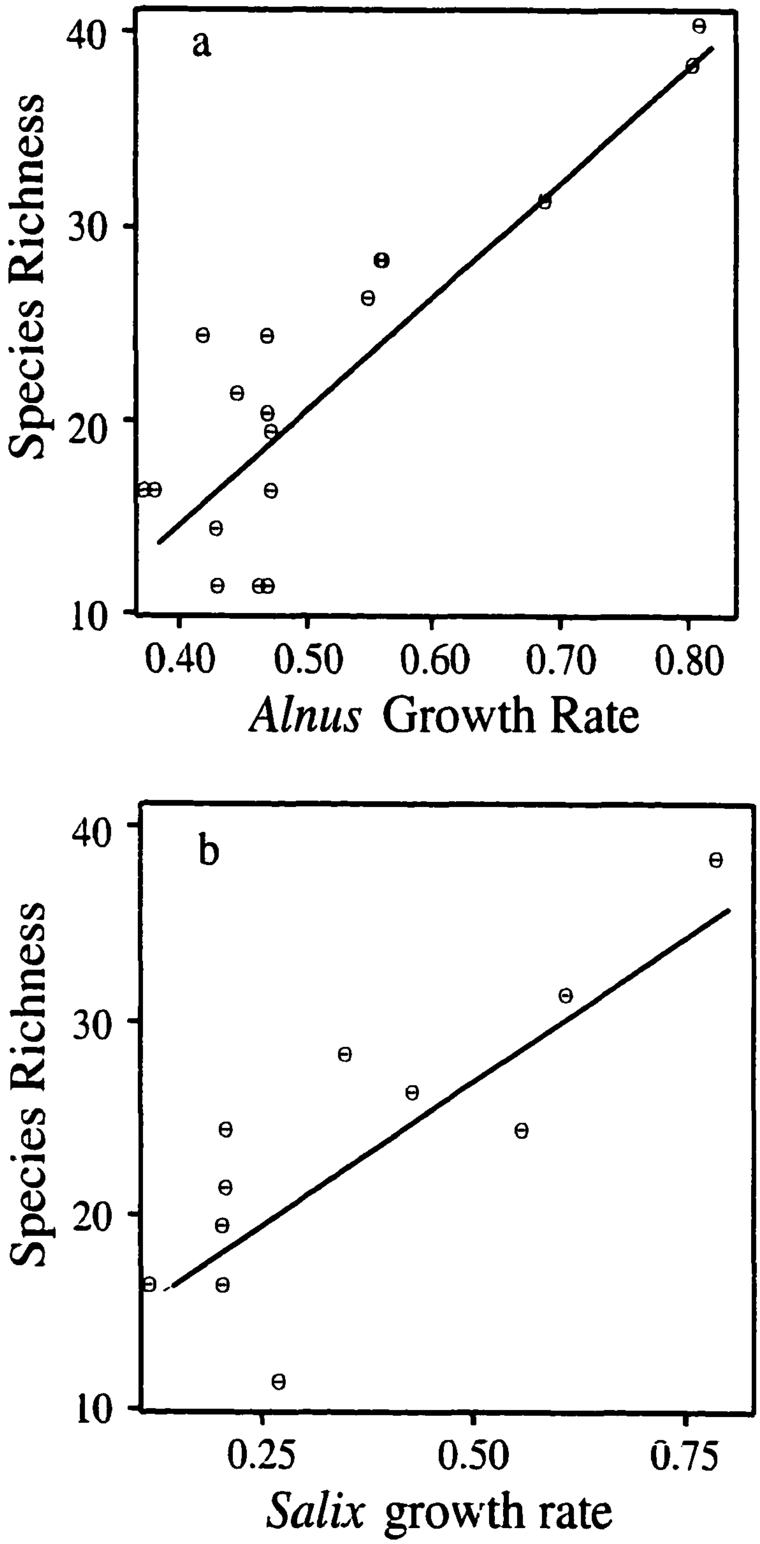
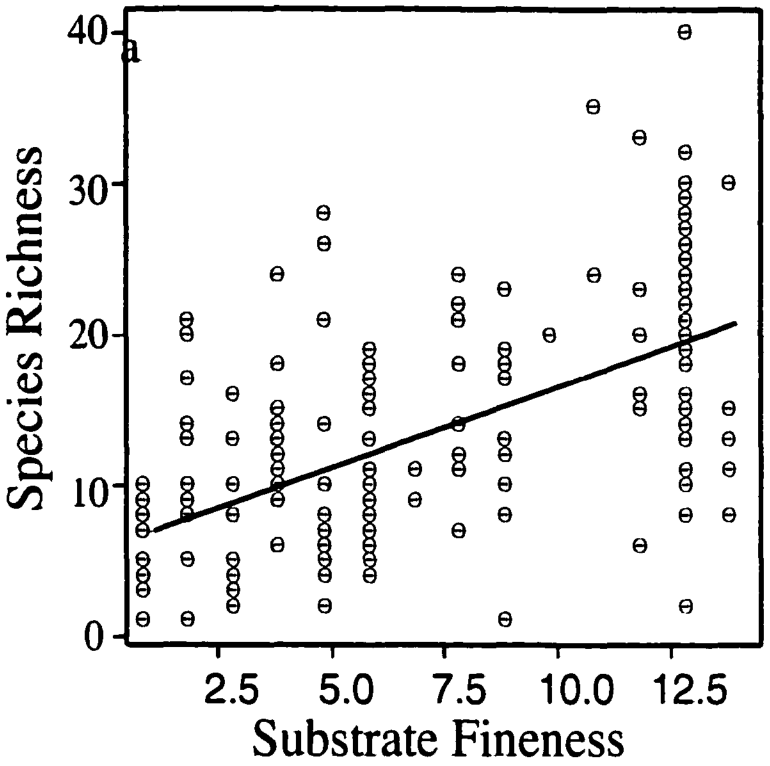


Figure 8. Growth rate vs. plot species richness on Talkeetna River (growth rate = cm*year^{-1}). (a) *Alnus* growth vs. plot species richness, $r^2 = .757$, $p < .01$, (b) *Salix* growth vs. plot species richness, $r^2 = .679$, $p < .01$.



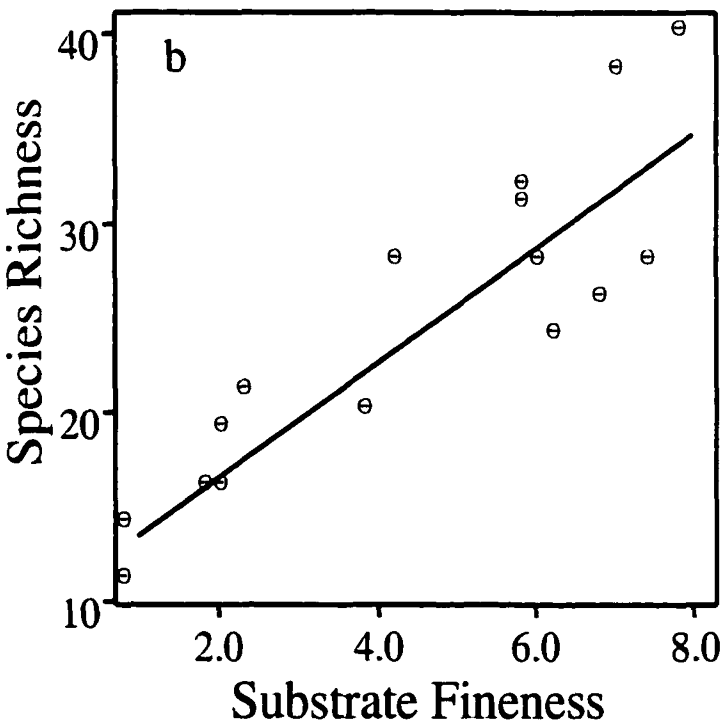


Figure 9. Species richness vs. substrate fineness on (a) Flathead River, $r^2 = .501$, $p < .0001$, (b) Talkeetna River, $r^2 = .810$, $p < .01$.

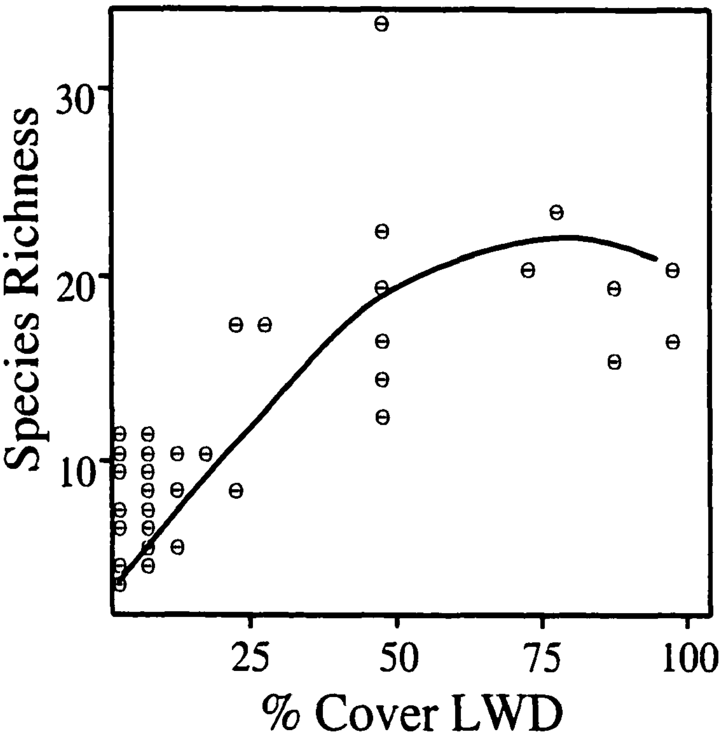


Figure 10. Species richness vs. percent cover of large wood debris in scour plain plots of the Flathead River. Line fitted with equation, $y = 3.87 + 454x - .0032x$, $r^2 = .656$, $p < .0001$.

THE CONSERVATION OF BIODIVERSITY ON FLOODPLAIN LANDSCAPES:

A VIEW FROM *SALICACEAE*

Abstract. The structural heterogeneity of alluvial flood plains characterized by native flow regimes functions to support the highest levels of terrestrial species diversity. Flow regulation that limits fluvial processes results in structural homogenization, and leads to impaired floodplain function. We use the habitat preferences and flow dependencies of characteristic *Salicaceae* species that play a disproportionately important role in structuring flood plains geomorphologically and biologically to evaluate current instream flow assessment techniques in light of their application in biodiversity conservation. While current river ecology emphasizes that flow variability inherent in native flow regimes is required to maintain or restore floodplain structure and function, none of the assessment protocols reviewed adequately allow for the quantification of system-specific instream flows needed by all *Salicaceae* life history stages.

Because floodplain habitat preferences of *Salicaceae* species are known and particular life history periodicities coincide with annual variability in flow regimes, instream flows that create and maintain *Salicaceae* habitats as well as sustain and disperse these species can be quantified from channel morphometrics. These instream flows should be reserved in unregulated river systems to provide for the conservation of *Salicaceae* species and the biological diversity they facilitate and support.

Key words: flow regimes, instream flows, fluvial processes, structural heterogeneity, *Salicaceae*, species diversity, flow regulation, biodiversity conservation.

INTRODUCTION

In unaltered states, river landscapes have extraordinary levels of species richness due to their long legacy of high spatial and temporal environmental heterogeneity (Ward and Stanford 1983, Ward 1998). Natural variability inherent in the native flow regime makes floodplains a mosaic of geomorphic surfaces created by fluvial processes that are dynamic in space and time. These four dimensional landscapes (longitudinal, lateral, vertical, and time, see Ward 1989) are unique in structure and function and support levels of species diversity uncommon in other terrestrial ecosystems (Naiman et al. 1993, see also Chapter 1). The maintenance of floodplain structure and function, and the conservation of constituent taxa are contingent upon the perpetuation natural variation inherent in the native flow regimes that characterize lotic systems in four dimensions (Ward 1989, Stanford et al. 1996, Poff et al. 1997). A compromise in natural flow regimes through regulation therefore results in homogenization of the complex nature of river landscapes and subsequently stymies system function and diversity (Ward 1982, Petts 1984, Walker 1995, Dudgeon 1992).

Although several studies have identified that flow variability inherent in native flow regimes is required to restore or maintain the structure and function of floodplains (see Stanford et al. 1996, Poff et al. 1997), studies have yet to propose a method that allows for the quantification of system-specific flow requirements identified by these general protocols. Quantitative efforts to identify instream flow (ISF) requirements to meet the needs of floodplain species and the creation of habitats they depend upon have largely focused on developing base flow requirements required by particular life history stages of a single species or communities of species, and particular geomorphic processes controlled by the flow regime within a limited temporal and spatial framework. While these are significant advancements, no one methodology has been developed to quantify the full range of flow variability required to restore the historical structure and function of floodplain ecosystems or maintain it prior to regulation. ISF assessment methodologies that identify the ISF requirements to maintain floodplain structure and function are needed on unregulated rivers to mitigate system degredation upon flow regulation as well as to develop a better understanding of what state regulated systems should be restored to. Studies focusing on the flow requirements during particular hydroperiods on limited spatial dimensions fall short of identifying the natural variability in native flow regimes that is needed to maintain the natural structure of floodplains and the diverse assemblages of species supported.

In this paper we use the biological requirements of the family *Salicaceae* to illustrate how ISF assessments aiming to quantify flow regimes required to maintain the functional integrity of floodplain ecosystems can be conducted. We first describe characteristic species of *Salicaceae* by describing their role as keystone species on floodplain landscapes, and subsequently, identify their dependence on the hydrologic and geomorphologic complexities of floodplain systems. Next, as *Salicaceae* habitats and influences on floodplains are impacted by river regulation, ISF assessments developed to quantify flow regimes necessary to preclude these impacts or restore floodplain habitats are reviewed, and lastly, we draw from these assessments to outline the fundamentals a new ecosystem-oriented approach.

SALICACEAE AS A KEYSTONE FAMILY

Viewing alluvial floodplains from the family *Salicaceae* allows for the functional interpretation of hydrogeomorphic processes operating on floodplains in space and time from a biological perspective. Specifically, the genera, *Populus* (Cottonwood) and *Salix* (Willow) are composed of species that are particularly well-adapted to the unique hydrogeomorphic factors and processes associated with floodplain landscapes. Species from this family typically dominate the shrub and tree canopies of North American floodplains and throughout all life history stages these species greatly influence a wide variety of plant and animal species as well as floodplain structure and function. *Salix* species initiate succession on young geomorphic surfaces, while *Populus* species develop forests and build surfaces with organic litter that are known to remain part of floodplain systems for 100 years or more. This successional sequence stabilizes and builds floodplain surfaces that eventually become the most species-rich terrestrial habitats. (Figure 1). As this sequence rarely succeeds without interruption on laterally migrating rivers, floodplains become a mosaic of age classes of vegetation patches leading to a complex landscape structure which is integral to species diversity patterns (Ward et al. 1999), as well as maintaining the availability of forage for wildlife. *Salicaceae* species on floodplain habitats have been shown repeatedly to be some of the most important browse species for large dominant herbivore species such as caribou (*Rangifer* spp.), moose (*Alces* spp.), elk (*Cervis* spp.), deer (*Odeocoilus* spp.), and beaver (*Castor* spp.) especially for moose (Stephanson 1995, Peek 1997) and caribou (Jakimchuk et al. 1987, Young and McCabe 1998) on Arctic and Subarctic rivers.

The influence of *Salicaceae* species extends beyond their life history at a given site of colonization and development. Erosional processes recruit individual trees and shrubs as debris within active river channels, where wood interacts with ISF to build geomorphic floodplain surfaces (Malanson and Butler 1990), influence local channel migration patterns (Nanson and Knighton 1996, Piegay and Gurnell 1997), and create critical habitats for many aquatic species such as trout (Hauer et al. 1999), salmon (Naiman et al. 2000), and many other species. Therefore, as species that play an integral role in the development, colonization, and transformation of geomorphic surfaces; the development of species rich plant communities providing critical seasonal habitats and unequalled foraging opportunities for many herbivores; and the development of instream habitats for many aquatic organisms, *Salicaceae* species should be considered as keystone species (sensu Paine 1966), as these species make an unusually strong contribution to floodplain structure and function.

The genus *Alnus* of the *Betulaceae* family is also important to note, though not considered as part of the *Salicaceae* keystone group. Some floodplains, particularly those of the Pacific Northwest, often have shrub communities dominated by *Alnus* species, namely *Alnus crispa*, *A. incana*, and *A. rubra*, species adapted to highly disturbed sites with high soil moisture. *Alnus* species are known to add significant amounts of nitrogen to the developing forest ecosystem, and consequently facilitate succession of floodplain surfaces from pioneer shrub communities to climax forest communities (Van Cleve and Viereck 1972). In fact, Walker (1989) showed that nitrogen accumulation in the top 2 meters of soil increased by nearly four times in 20 years of developing alder stands on floodplains in the interior of Alaska. Although

Alnus species do not influence floodplain systems in as many ways as *Salicaceae* species, they are mentioned within the current paper as they often make significant contribution to the structure and function of many floodplain systems, especially those relatively limited in nitrogen as many northern floodplain systems are.

Considering the influence of these species on floodplain character, a rich literature as well as empirical observations from two large North American floodplains on the Middle Fork Flathead River, Montana, and the Talkeetna River, Alaska, on *Salicaceae* and *Alnus* species is discussed to highlight the specific habitat associations of these species as well as the dependence of all life history stages on particular instream flow characteristics. To provide the basis for this discussion, the geomorphological template of floodplains and influential fluvial processes are described. Once the dependence and influence of these species has been described on these systems, the adverse affects of river regulation will be considered from the perspective of *Salicaceae* conservation.

FLOODPLAIN GEOMORPHOLOGICAL TEMPLATE

ISF PATTERNS AND DEBRIS PROCESSES

Local floodplain morphology is determined by the legacy of flooding (Poff et al. 1997, Ward 1998). Big floods are largely responsible for local floodplain morphology, as they erode surfaces laterally and vertically, resulting in a wide variety of channel types (figure 2) and zones of groundwater – surface water exchange (Wondzell and Swanson 1999) that may persist for long periods of time until the next big flood (Stanford et al. 1996). In the interim more regular flow dynamics maintain a gradient of connectivity with the wide variety of channel morphologies embedded into the active floodplain during by the last big flood. These interim flow dynamics, however, also have the capacity to do geomorphic work, and often gradually or even subtly reconfigure floodplain surfaces and channel structures (Stanford et al. 1996). For example, mean annual peak flows are sufficient to recruit large woody debris and transport it downstream. In many alluvial systems this processes results in the formation of large debris complexes that may greatly influence sedimentation, channel migration, channel avulsion, and the development of vegetation within the active floodplain (Malanson and Butler 1990, Maser and Sedell 1994, Naiman et al. 2000). In high latitude river systems, ice processes perform similar roles. During break up periods, ice transport often results in the formation of large ice jams that impede flows and influence localized scouring, over bank flooding, and even channel change (Prowse 2000), especially in Arctic systems, where peak flows and sediment transport coincide with break up. Ice has also been documented to provide for extreme scouring of floodplain surfaces clean of established vegetation, where the lower limits of woody plant colonization are often controlled by ice processes (Prowse 2000). Though these processes should be considered secondary in influence to big flooding events, the interaction between debris and instream flow can result in large-scale disturbances that characterize floodplain morphometry and established vegetation patterns (Prowse 2000, Mouw 2000, Poole et al. in review). These disturbances, however, are typically extended to specific points on longitudinal river axes, whereas extreme floods reshape alluvial river reaches throughout entire catchments.

EXPANDING THE DEFINITION OF FLOODPLAINS

Although the extent and complexity of floodplain landscapes is dependent upon local hydrogeomorphology, lotic systems are characterized as an extensive interconnected hierarchy of hydrogeomorphic habitats and gradients of which primary river channels are only a part (Ward 1998). Current literature encourages an expansion of our characterization of river ecosystems to include often-extensive arrays of channel morphologies and interacting groundwater, or hyporheic zones (Stanford and Ward 1993, figure 3). Across lateral and longitudinal floodplain dimensions, erosional processes controlled by laterally migrating river channels form a wide variety of aquatic habitats. Active alluvial river reaches are often characterized by multiple channel types flowing around alluvial islands that are highly transient relative to geomorphic surfaces along meandering or constrained reaches. Two diverging primary channels often form large islands; where as smaller islands are often created by smaller backbar channels that are seasonally connected to primary channels. Paleochannels are formed during avulsive events when channels are abandoned, or via lateral channel migration over time. Though these channel types are most often surficially disconnected, they often receive groundwater discharge and may flow seasonally or throughout the entire water year. These spring brooks have different thermal and chemical properties than channels with surface connection, as groundwater feeding these channels is thermally buffered and is often richer in N and dissolved organic C (Ford and Naiman 1989), presumably due to microbial activity within hyporheic zones (Fiebig et al. 1990, Stanford and Ward

1993). Expanding the boundaries of floodplain ecosystems to include these interacting aquatic habitats has great implications to the management of flow dynamics driving connectivity across these landscapes via surface and subsurface hydrogeomorphic interactions.

DYNAMIC EQUILIBRIUM OF FLOODPLAIN GEOMORPHOLOGY

In free-flowing systems with relatively consistent hydrodynamics and subsequent fluvial dynamics, floodplain morphometrics remain within a dynamic equilibrium (Wolman and Leopold 1957). Though channel migration and island formation is a dynamic processes, relative elevations of channel morphologies remains rather consistent over time. Specifically on longitudinal floodplain axes, where side channels, back-bar channels, and spring brooks show a consistent elevational relationship on vertical floodplain axes (Poole et al. 2001). Whereas secondary channels are higher in elevation than primary channels at their origin, spring brooks are typically lower in elevation than primary channels. Specifically, seasonal overflow channels are the result of localized head cutting at flood stages, and springbrooks are typically deeply incised, many of which are the result of flow in past river channels that have recently migrated laterally to occupy other portions of the present-day floodplain. Thus, these fluvial processes can be described as a dynamic equilibrium where current flow and sediment regimes explain the dynamics of this process. For example, during extreme floods, river channels are known to widen and side channels are flushed or created. During interim flows, scour and fill processes are perpetuated and sedimentation on riverbanks and within side channels causes channels to narrow and side channels to fill (Petts and Amoros 1996) providing for successional progression within these habitats. This dynamic fluvial process then highlights the importance of extreme and interim events, and because over time the relative vertical positioning of these channel morphologies remains in a dynamic equilibrium, present-day floodplain morphometrics can be relied upon to assess those flow dynamics which perpetuate connectivity across the landscape throughout time.

Terrestrial floodplain surfaces are also diverse, and have sediment structures determined by fluvial processes which may be erosional or depositional in nature. The diverse topographical structure of floodplains results in the mosaic of scoured and aggraded surfaces, which shift over time due to the unconsolidated nature of floodplain alluvium and spatial variation in stream power during flooding events. The size and composition of these surfaces (like islands) is largely controlled by peak flow events, though debris and colonizing vegetation influence fluvial processes such as scour and deposition at smaller scales within these surfaces.

PLANT RESPONSE TO FLOODPLAIN MORPHOMETRY

PARADIGMS IN RIPARIAN VEGETATION

It has been repeatedly stated that riparian vegetation exhibits distinct zonation patterns from channel to uplands, resulting in broad-scale segregation patterns of species along a floodplains elevational gradient (Ward 1998, see figure 4). Though this has been repeatedly shown for many river systems (Nilsson and Berggen. 2001), vegetation zonation on alluvial floodplains is not as straightforward (figures 5 a, and b, see also Chapter 2) as environmental gradients are patchy or highly variable rather than continuous. Data from the Talkeetna River show that floodplain habitats are not aligned in a continuous fashion along flooding disturbance (frequency of flooding) gradients (see Chapter 2). Indeed, many sites analyzed from the same data set show that sites of the same elevation might be scoured or aggraded, as flood frequency and power are anisotropic in space. Thus on active alluvial floodplains, elevation above active channels is not a consistent predictor of vegetation community structure, nor are all life history stages of plant species dependent upon flooding frequency or inundation duration. Rather, the presence of these species is dependent upon habitats created by extreme flow events and the levels of connectivity achieved between primary channels and *Salicaceae* habitats during interim flows on all floodplain dimensions (discussed below). Current approaches to explain the distribution and abundance of floodplain plants should be expanded to look at the geomorphic habitats of plant species and how they are created and maintained by the current flow regime, as well as the flow dependence of all plant life history stages.

FLOW DEPENDENCIES OF *SALICACEAE*

LONGITUDINAL AND LATERAL DIMENSIONS

First to note is that the reproductive and population biology of these species is directly responsive to hydrogeomorphic patterns and processes of floodplain landscapes. Both *Populus* and *Salix* species are known to disperse seed during annual peak flows, regardless of macro-climate (see Poff et al. 1997). On the Flathead River, seed dispersal coincides with peak flows in early June, while coincidence dispersal of these species comes in late June on the Talkeetna River when peak flows are typically reached (personal observation). While both *Populus* and *Salix* species are primarily wind dispersed, fallen seed is transported by water and sown in sediment deposits during stage decline. Thus the spatial extent of seedling dispersal is directly related to river stage during annual flooding. While the transport and location of seed deposition may be somewhat stochastic, the germination, establishment, and development of seedlings is largely contingent upon the nature of the habitat template upon which seed is sown (Mouw 2000, see discussion below), not the *frequency* in which the site is flooded. In both genera, seedling establishment and success is largely contingent upon soil moisture (Krasny et al. 1988a).

Beyond these generalities among the genera *Populus* and *Salix*, a distinction in habitat preference can be made based upon ecophysiological bases. Though the genus *Salix* displays a broad ecological niche, many species have physiological adaptations allowing the toleration of anaerobic conditions, as *Salix* species have to ability to form adventitious roots in relatively deep and poorly drained sediments (Krasny et al. 1988b). Further, *Salix* species show root suckering that increases with soil moisture. These physiological adaptations allow for the colonization of *Salix* species on relatively low elevations and within poorly drained sediments. These habitat preferences lead to the colonization of *Salix* species within or near secondary aquatic habitats, such as back-bar channels, paleochannels, backflow habitats, and scour pools. Thus on lateral and longitudinal floodplain dimensions, *Salix* species are patchily distributed and are best represented at sites where stream power is reduced to provide for deposition of fine sediments during flooding, and where soil moisture is high (Mouw 2000). These habitat preferences restrict Salix colonization to sites associated with secondary channel types on the lateral dimension, while on longitudinal dimensions, *Salix* abundance and richness increases on overflow channels from channel origin to its confluence with primary channels where backflow conditions occur; again, representing a stream power gradient (figure 6). Thus, the proliferation of current distribution and abundance patterns of these species is strongly dependent upon the maintenance of connectivity between primary and secondary channel morphologies during the growing season. Further, aggressive colonization of secondary aquatic habitats in response to interim connectivity flows should be seen as a critical process accelerating succession within these channel matrices (Edwards et al. 1999). As this successional process occurs within much smaller time scales than return intervals for extreme flushing flow events (Petts and Amoros 1996), *Salicaceae* species play a vital role in the dynamic equilibrium of floodplains geomorphology.

As *Populus* species prefer well-drained substrates for establishment and development (Krasny et al. 1988, Merigliano 1996) they occupy very different floodplain sites. As with *Salix* seedling establishment, *Populus* colonization is dependent upon flooding. As a result of *Populus* substrate preferences and their dependence upon flooding for renewal, these species become established on floodplain surfaces that experience greater stream power during flooding. In general, *Populus* is best represented on sites with sandy substrates (Krasny et al. 1988), though they are also found on a variety of substrate conditions, excluding only those sites with poorly drained, fine sediments. The coincidence of *Populus* seedling establishment with extreme flooding events (Merigliano 1996, Rood and Mahoney

2000) indicates that *Populus* forest regeneration is episodic and largely dependent upon the infrequent and extreme floods. Though vegetative reproduction does occur on relatively dry sites during interim flow periods, the extent of *Populus* seedling establishment on the lateral dimension is entirely dependent upon the magnitude of floods. On the Talkeetna River, the most recently established cohort is 14 years old showing that the establishment of this cohort stems from the extreme flood of 1986 which was nearly 900% of mean annual flow (personal observation).

Many *Salicaceae* floodplain species also are known to resprout from root or shoot fragments, or both (Krasny et al. 1988a). Woody debris transport during flooding, then, is also a means of dispersal for these species. In fact, vegetative reproduction by these means is common, even from very large *Populus* trees transported and covered entirely or partially by river sediments on both the Flathead and Talkeetna Rivers (personal observation). Excavation of these vegetatively reproduced shoots shows attachment to whole trees or smaller debris of the same species. This means of dispersal to floodplain surfaces is also directly dependent upon floods and the extent of this dispersal on flood magnitude.

VERTICAL DIMENSIONS

Though riparian plant ecologists have intensively investigated lateral and longitudinal hydrogeomorphic patterns and processes and plant responses, vertical dimensions have been largely ignored (Stanford et al. 1996). Recent literature has shown that GW-SW interaction is critical to understanding the establishment of woody vegetation and subsequently plant productivity (Rood and Mahoney 1990, Stomberg 1993). These studies show that while fluvial patterns largely control the establishment of woody floodplain species, gradients in hydrology on the vertical axis ultimately explain the success of *Salicaceae* species recruitment to a given surface. Thus, depth to water table is an important vertical gradient explaining vegetation zonation and bioproduction. Plant ecologists have largely ignored the fact that vertical hydraulic gradients (VHG) are dynamic in space, and on many alluvial floodplains, complex gradients in VHG have been observed (figure 3, see also Chapter 2). Freshwater ecologists have recognized for decades that groundwater discharge has a profound influence on instream biotic communities (Stanford and Ward 1993). Indeed plants respond to this gradient as well, and often form communities higher in species richness at upwelling sites (see Chapter 2). The growth of *Salicaceae* and *Alnus* species also differs greatly between sites characterized by upwelling groundwater and downwelling stream water (Harner and Stanford, in review, see also Chapter 2), where growth rates are typically much higher at upwelling sites than downwelling sites. Whether this response is driven by water availability or nutrient differences has yet to be determined. What is clear is that river stage cannot be used as a surrogate for alluvial aquifer stage, and contrary to current thinking, GW – SW interaction in not unidirectional. Nonetheless, as aquifer stage is often directly responsive to instream flow dynamics (figure 7) interim flows must be sustained at levels sufficient to maintain aquifers supporting current riparian vegetation in their respective habitats, which will be discussed below.

RIVER REGULATION

GEOMORPHIC RESPONSES

An estimated two-thirds of freshwater flowing to oceans is regulated by approximately 40,000 large dams and more than 800,000 smaller ones (Petts 1984, McCully 1996, Nilsson and Berggen 2000). Comparative studies of free-flowing and regulated rivers have increased our understanding of the environmental consequences of dams (Nilsson and Jansson 1995, Rosenberg et al. 1995). The impact of a single impoundment can affect flow dynamics along the entire river and subsequently modify floodplains and their biotic communities (Nilsson and Berggen 2000).

First to note, is that regulation typically reduces flood peaks, and displaces them in time (Petts 1984, see figure 8). Such influences reduce over-bank flooding, and subsequently the frequency and timing of floods. Other flow characteristics are significantly modified, such as increased base flow levels, and rates of stage fluctuation (ramping rates). Sediment flux though these systems is also impeded, as dams trap sediments that would otherwise be eroded and transported throughout the longitudinal river axis.

These changes adversely affect geomorphologic floodplain processes. Below dams water tends to restore its original load of sediment and nutrients, resulting in increased erosion and channel incision. Such erosion leads to channel simplification and reduced geomorphologic activity on floodplains, such as reduced point-bar development, and reduced channel migration (Johnson 1992, Polzin and Rood 2000). This channel simplification and incision disconnects a river from its floodplain in two main ways. First surficial connectivity is significantly reduced as primary river channels have a limited connection with secondary channels and other aquatic habitats, such as spring brooks, and pools. Second, channel incision significantly lowers floodplain aquifer tables, further limiting connectivity between primary and secondary floodplain habitats due to impaired subsurface GW – SW interactions (Pinay et al. 1990, Nilsson and Berggen 2000).

PLANT RESPONSE TO RIVER REGULATION

Reduced peak flows after regulation significantly narrows the spatial extent of seedling dispersal on the lateral dimensions of floodplains. Further, displacement of peak flow events in time is likely to further limit dispersal of *Salicaceae* species which have reproductive cycles coinciding with historical peak flow events. Although such concerns have been expressed for fish and wildlife showing similar life history stages that are flow dependent, this is rarely considered for plants, even in recent literature. Reduced peak flows also significantly alter cut and fill dynamics required on floodplain surfaces and within secondary aquatic habitats to rejuvenate succesional patterns of *Salicaceae* species. Over time, these habitats have been shown to "terrestrialize" and become colonized by upland species (Ward 1998, Stromberg et al. 1996). Such a disconnection has been shown to significantly reduce biodiversity within extant floodplain habitats as well. Loffler (1990) showed extreme reductions in species richness of aquatic macrophytes, mollusks, and fishes when river channels are disconnected from floodplain habitats. Specifically, reductions in species richness of greater than 50% were observed with these organisms. Such differences are also likely for *Salicaceae* species, which are dependent upon this connectivity to maintain adequate water and sediment relations. In fact, this disconnection has shown drought-induced mortality in *Populus* species on several rivers (Rood and Mahoney, 1990, Rood et al. 1994). Further, the lowering of water tables induced by flow reductions has been shown to cause floodplain plant communities to shift from *Salicaceae* dominance to dominance by species adapted to drought or those more common in upland habitats (Pinay et al. 1990, Stromberg et al. 1996).

FUTURE NEEDS IN RESEARCH

While responses of *Salicaceae* dominated plant communities to river regulation is well documented, ISF assessments accounting for all life history stages of species, and their specific habitat preferences are rare. Such assessments are vital to our understanding of the dependence of these species on hydrogeomorphic floodplain factors and processes. Further, ecophysiological studies of these species typically operate on one or perhaps two floodplain dimensions. While the objective in many studies is often to better understand abiotic influences operating on a single dimension, the development of conservation strategies for floodplain flora can only be successful if the four-dimensional nature of lotic systems (*sensu* Ward 1989) is accounted for.

INSTREAM FLOW RESERVATION FOR FLOODPLAIN VEGETATION

Given the costs associated with disconnecting a river from its floodplain, it is currently critical to develop methodologies that quantify flow regimes required to sustain floodplain vegetation on northern rivers prior to rises in competitive uses of ISF, which is already taking place (Estes 1998). In the 1980's several large hydroelectric projects were proposed for the Susitna River, and plans for this development are currently resurfacing.

The current literature is rich in studies proposing restoration protocols and ISF assessment methodologies. Indeed there are a wide variety of tools from which to select or assemble methods for ISF assessment (see Hardy 1995 for an in-depth review). Here, a handful of methods are selected and evaluated in light of their use in quantifying instream flows required to sustain current floodplain vegetation characteristics on the aforementioned rivers. Methodologies range from defining flow regimes responsible for large-scale zonation patterns in vegetation cover types on riparian elevational gradients to three-dimensional approaches that assess floodplain morphological changes over a variety of discharges with GIS technologies. Here, we draw from four general approaches across this spectrum.

In bedrock-confined river systems, where vegetation cover types are aligned along disturbance continua, hydraulic model development allowing for plant cover types to be positioned along gradients of inundation duration has been successful at making predictions in vegetation change in response to flow alteration (Franz and Bazzaz 1977, Auble et al. 1994). However, as the occurrence of dominant vegetation cover types cannot be predicted along elevational gradients on active alluvial floodplains this approach cannot be applied here, or within alluvial floodplains in general. What is needed is an approach that quantifies flows needed to sustain the connectivity between a river and its floodplain achieved during peak flow events and interim flood flows. Also needed, is an approach that adequately addresses the quantification of flows required to maintain aquifer stages supporting riparian vegetation or rates of stage decline. Specifically, an approach is needed which accounts for all critical flow characteristics influencing life history stages of *Salicaceae* species.

First, addressing aquifer stages and rates of decline, the methodologies of Rood and Mahoney (1990) show that alterations in stage decline due to river regulation have catastrophic affects to *Populus* seedlings. They show that at sites receiving inundation and subsequent seedling recruitment, flow drawdowns typical of regulated rivers ultimately prohibits the recruitment of *Populus* seedlings. Further, the work of Stromberg (2001) shows that productivity (growth rates) of woody species is greater at higher discharges, further showing that connectivity between instream flows and aquifer stages is a critical consideration when quantifying needed interim flows to support recruitment and productivity of woody floodplain vegetation.

Though these studies highlight the importance of linkages between stream water and groundwater to plants, and allow for the quantification of stage levels and decline rates needed to sustain and recruit woody plant species, these approaches must be used in concert with methodologies quantifying flows needed for the maintenance of surficial floodplain connectivity and fluvial processes creating floodplain habitats.

Stanford et al. (1996) construct a general protocol for the restoration of regulated rivers, on the basis of restoring flow dynamics that at the very least, mimic historical flow dynamics prior to flow regulation. They draw from empirical studies on regulated and free-flowing rivers to show that re-regulation to mimic historic flow dynamics should be the first step to reconnect rivers with disconnected floodplain habitats. Further, they suggest that beyond costs associated with power generation, restoration efforts come at low cost, because the river can do most of the work. Such a methodology addresses the need for peak flows to re-establish the process of cut and fill alluviation; processes which create suitable habitat for *Salicaceae* species. Although this protocol is geared toward restoration efforts, such a protocol can likewise be developed prior to regulation, allowing an assessment of flow characteristics and levels maintaining current distributions of vegetation on free-flowing systems.

Yet another approach to ISF assessment has recently been proposed by Richter and Richter (2000). Theirs is a proactive approach aimed at directly quantifying flows effective to perpetuate the lateral migration of the Yampa River. Using aerial photography they propose a methodology that monitors channel migration over the current range of flow characteristics to show that time of duration at 125% of bankfull discharge is the variable explaining channel migration rather than magnitude of peak flows. Such an approach greatly increases the ability of managers to spatially and temporally quantify the effects of regulation or re-regulation of flow dynamics to habitat forming fluvial processes. However, if this approach is singly relied upon, there is great risk of reserving those flows creating floodplain habitats, yet not accounting for flow characteristics required to maintain connectivity. Stage declines and post-peak stages are also not addressed, indicating that seedling recruitment may not be achieved considering the findings of Rood and Mahoney

(1990). Further, they suggest that upon reaching effective flows, surplus water could be available for human use and still maintain lateral migration processes. While these particular processes may perpetuate, dispersal of seedlings may be greatly narrowed in space, as surfaces flooded beyond stages reserved for lateral migration would lose the capacity to regenerate *Salicaceae* forests and shrub communities. Further, these flows are important to create new habitats and flush existing aquatic habitats to maintain their successional vigor.

FUTURE DIRECTIONS IN ISF ASSESSMENT

Future assessments of ISF requirements in free-flowing river systems, should draw from the above approaches to construct methodologies that account for natural flow variability and all plant life history stages. Proactive approaches in regions where current water laws allow ISF reservation for the purposes of sustaining fish and wildlife habitats should be taken to quantify how much current day hydrographs can be modified and yet maintain the diversity of floodplain habitats and constituent taxa.

First, habitats of all species in concern must be recognized, as well as the population dynamics within these habitats. Second, the ISF dependence of all life history stages of these species must be recognized, as previously demonstrated with *Salicaceae* species. Lastly, patterns in connectivity between river channels and these habitats of floodplain species must be quantified and understood.

IDENTIFYING PEAK FLOWS

To develop a successful ISF reservation, the first challenge will be to quantify stages of peak and interim flood flows responsible for aquatic – terrestrial connectivity. This can be conducted from two general approaches. First, managers can rely on the evidence of past flooding events within the local vegetation. Second, use of daily flow data from the entire period of record may also be sufficient given an adequate period of record (discussed subsequently), which is rare on northern rivers outside of the continental U.S. Where adequate data is not available, it has been shown that *Populus* species can be used as indicators of past flooding stages, as their recruitment is episodic (Merigliano 1996, Rood and Mahoney 2000). Ideally, these two techniques should be used in concert to confidently delineate the stage of extreme events, as *Populus* species may exist on terraces flooded by the river during earlier climatic periods, and could be the result of vegetative reproduction over very long periods of time. If *Populus* cohorts are found to age back to certain flooding events, and the modeled stages of those events, then greater confidence is gained in quantifying and predicting stages of extreme events. For example, the youngest *Populus balsamifera* cohort found on the Talkeetna River, is 14 years old, and is presumed to have established by the extreme event of 1986, when the river peaked at 63,200 cfs. What is most interesting about this event is that it occurred in the fall and did not coincide with seed dispersal for this species. As a result, the 14-year-old individuals are a result of vegetative reproduction from *Populus* debris transported during this event, although some seedlings of the same age are present on some surfaces (personal observation). What is critical to note here, is that this event is not only responsible for much of the present day morphology on this system, but the dispersal of *Populus balsamifera* to surfaces that are flooded only once every 74 years as predicted by locally developed rating curves and the full period of record from USGS gage #15292700 (see Chapter 2). During this event all active floodplain surface elevations were flooded, even the relatively old *Populus* – *Picea* forests that fringe the floodplain. On the South Fork Snake River, this approach proves to be even more fruitful. With a 86-year period of flow records, this approach was used to show that the maximum age of uniform *Populus angustifolia* stands are aged to large floods on this system (Merigliano 1996).

IDENTIFICATION OF INTERIM FLOWS

Flow stages achieving interim connectivity and the facilitation of successional progression can be defined by local channel morphometrics, namely channel width, depth, and elevation, as these variables are directly responsive to gradients in connectivity with primary channels (Petts and Amoros 1996). That is, narrow and shallow channels (annually flooded) are relatively high in elevation and are the least connected with primary channels, as they annually receive flow only during the highest annual flows. Therefore, in terms of flood stages responsible for connectivity, it can be argued that flow reservations reserving flows providing for connectivity within these channels may account for connectivity in all channels. Flood stage is only one important flow characteristic, however. Flood frequency, duration, timing and flow variability (mean daily change or mean daily percent change in flow) are also necessary flow attributes maintaining connectivity and channel maintenance processes operating at natural rates (discussed subsequently). However, simply monitoring the stage at which these removed channels become connected on gauged systems allows for a full ISF assessment, as once this "effective" stage is quantified the period of flow records can be utilized to quantify flow characteristics associated with target flows. Such an approach is quite simple, and can be conducted by on-site observation, or within a GIS framework. The later approach is likely to allow for more confident estimates of effective stage observations across entire floodplains (discussed subsequently).

In addition to connectivity flows, interim peak flows, or *flushing flows* should be quantified. Here, we define flushing flows as the mean daily peak flow during the hydroperiod in which connectivity is achieved. As interim periods are largely characterized by flows that maintain forward successional progression, peak flows are also an essential part of the flow regime during these hydro-periods (as previously mentioned). Without interim peak flows, floodplain succession will likely proceed at un-natural trajectories, and therefore, reservation strategies must also include these events at their natural duration and timing (defined below). Below we use on-site field observations from May – September 2000 on the Talkeetna River to demonstrate this approach as a federal reserve water right already exists for the Middle Fork Flathead River. The demonstration should only be considered an example of how such a proactive ISF assessment could be applied to unregulated alluvial rivers, rather than an actual proposed reservation for this system. In addition, as all river systems are unique, only the general approach described here is applicable to other systems.

RESERVATION OF ISF REGIMES

To determine connectivity or "effective" flows, stage – discharge curves (see Auble et al. 1994, Pollock et al. 1998) may be developed at river cross sections corresponding to seasonally active overflow channels. These curves are then used to predict at what discharge, levels of connectivity are achieved. Alternatively, with some knowledge of the river hydrograph, simple qualitative on-site observations may suffice. That is, an observer simply notes the day and time initial connectivity between seasonal and primary channels is achieved, allowing reference to the recent flow records at nearby gauging sites to identify effective connectivity flows. Subsequently, observations of bankfull discharge (see Gordon et al. 1992 for definition) are made, as at these flows it is assumed that channel maintenance processes are at adequate levels to maintain connectivity with primary channels and perpetuate natural rates of succession (Petts and Amoros 1996).

A promising alternative strategy is the use of aerial photography within a GIS framework (see Benke et al. 2000). Aerial photos taken at a full range of discharges entered into a GIS allow the quantification of percent inundation on floodplains in a spatial context. Further, as demonstrated by Richter and Richter (2000) photography from a sufficient period of record allows quantification of fluvial processes and their dependence on particular hydrologic variables.

In conjunction with these techniques of monitoring "effective stages", flow duration curves (see Figure 9) are developed to determine the natural duration of effective flows, as any reservation of an ISF should at the very least mimic the natural hydrograph (Stanford et al. 1996). Although connectivity flows being reserved may be below probable river stages for some water years, flow duration, timing and daily rates of change associated with these flows are not compromised. The timing of connectivity flows is determined by the period of record, where daily flow statistics are utilized (see application section). As previously mentioned, timing of these flows is critical to the reproductive biology of *Salicaceae* species. Also important is flow variability that determines how quickly target flows are reached. Daily flow statistics are also utilized to quantify natural rates of daily changes in flow. These rates are considered a critical part of any reservation as floodplain biota have adapted to natural variability inherent in the native hydrograph. Interim flushing flows and extreme floods are quantified in a similar manner. As with connectivity flows, the flow duration curve is used to determine the flow characteristics of these flows, and their timing defined from the entire period of record.

APPLICATION

On the Talkeetna River, connectivity flows are reached at 17,000 cfs as determined by flow characteristics within back-bar channels at four river cross sections spaced approximately 2-3 km apart (see Mouw et al. 2001). These channels were selected as they were seasonally active and the highest in elevation with respect to the main channel and were assumed to be the least connected. Indeed personal observation of flooding showed this to be true. At 17,000 cfs all four channels were roughly at bank full flow, and at this stage it is assumed that channel maintenance processes are at adequate levels to maintain connectivity with primary channels and perpetuate natural rates of succession. Therefore, for interim connectivity flows, a reservation of 17,000 cfs should be made. Using the flow duration curve we see that this flow is equaled or exceeded six times a year when the 36 years of data are utilized from USGS station #15292700 (figure 9). Analysis of daily flow statistics shows that 17,000 cfs is the 85th percentile flow (15 percent of flows exceeding this volume) typically arriving in early June where it is reached four times, and twice again in mid-August (figure 10). Mean daily changes in flow during these hydroperiods are quite extreme. In order to mimic the native hydrograph, daily changes in flow should be determined from the period of record. Once quantified, daily rates of change determine how quickly target flows should be reached, and at what point in the season flows should begin to increase. In other words, they characterize flow variability as target flows are reached and receded from, and should be included in a reservation to avoid ramping or peaking if the system should become regulated.

In addition to connectivity flows, interim flushing flows are reserved. On the Talkeetna River this flow is 21,000 cfs (defined above), and is equaled or exceeded two times a year. Observing the daily flow statistics we see that this flow is the 90th percentile flow typically returning in early June when *Salix* species are dispersing their seed (figure 10). Once again, flow variability for the hydroperiods before and after this flow is reached at its natural duration need to be included in the ISF reservation.

Extreme flow events come to the Talkeetna River during late summer and early fall. Of the two most extreme events, one was in August (1971) and the other in October (1986). As the timing of these events greatly affects the biology of

Salicaceae species, care must be taken in their reservation. First, extreme events must be defined, and subsequently their timing addressed. As on the Talkeetna River all active floodplain surfaces (all surfaces below *Populus – Picea* gallery forests) become inundated at 40,000 cfs (see Chapter 2), we determine all flows during the period of record equaling or exceeding this stage as "extreme" events. This flow has been equaled or exceeded six times over 36 years and therefore has a return interval of 1.6 times every ten years. We would include this flow on its average timing and frequency in the reservation. As this flow typically comes at the end of the growing season, the main function of this flow is to flush the system of sediment, and sculpt new floodplain surfaces and habitats. Daily rates of change associated with extreme flows are not as critical as with connectivity flows, as they typically last only a day or two.

Using the approach we have outlined, a reservation could be developed that asks for annual flow volumes that do not exceed average total annual flow for a given system, and still accounts for all target flows at their natural duration without exceeding daily rates of change typical of the system.

CONCLUSION

The above-suggested ISF reservation strategy addresses floodplain biodiversity conservation by recognizing the flow dependence of *Salicaceae* habitat forming and maintenance processes on alluvial floodplains. Implementation of this strategy should maintain floodplain biodiversity by sufficiently accounting for: 1) the creation of floodplain habitats, 2) the maintenance of successional vigor in existing habitats, 3) the reproduction, dispersal, recruitment, and maintenance of *Salicaceae* species, and 4) perpetuation of lateral channel migration processes and consequently the recruitment of LWD to complete the *Salicaceae* life cycle. It must be stressed, however, that the effects of this protocol must be viewed as a hypothesis, as any modification to the virgin flow regime will likely cause channel change, and compromise floodplain vegetation. However, short of reserving virgin flows, the approach defined here attempts to define a bare-minimum flow regime that creates floodplain habitats, and provides for base levels of connectivity with these habitats. Such a flow regime is expected to maintain floodplains in a state of dynamic equilibrium in space and time.

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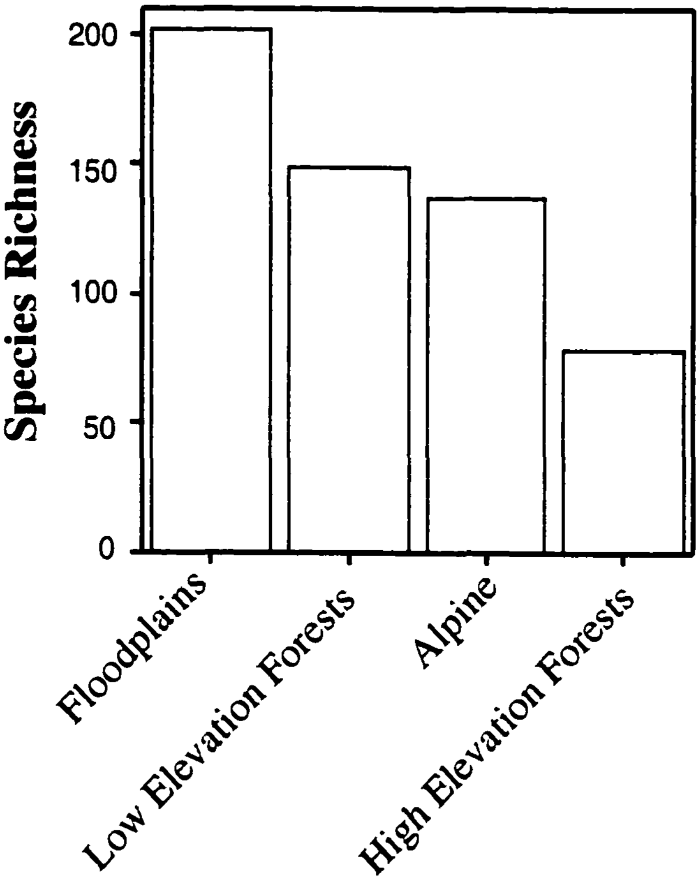

Figure 1. Species richness by ecosystem types sampled on the Middle Fork Flathead Catchment (adapted from Chapter 1).

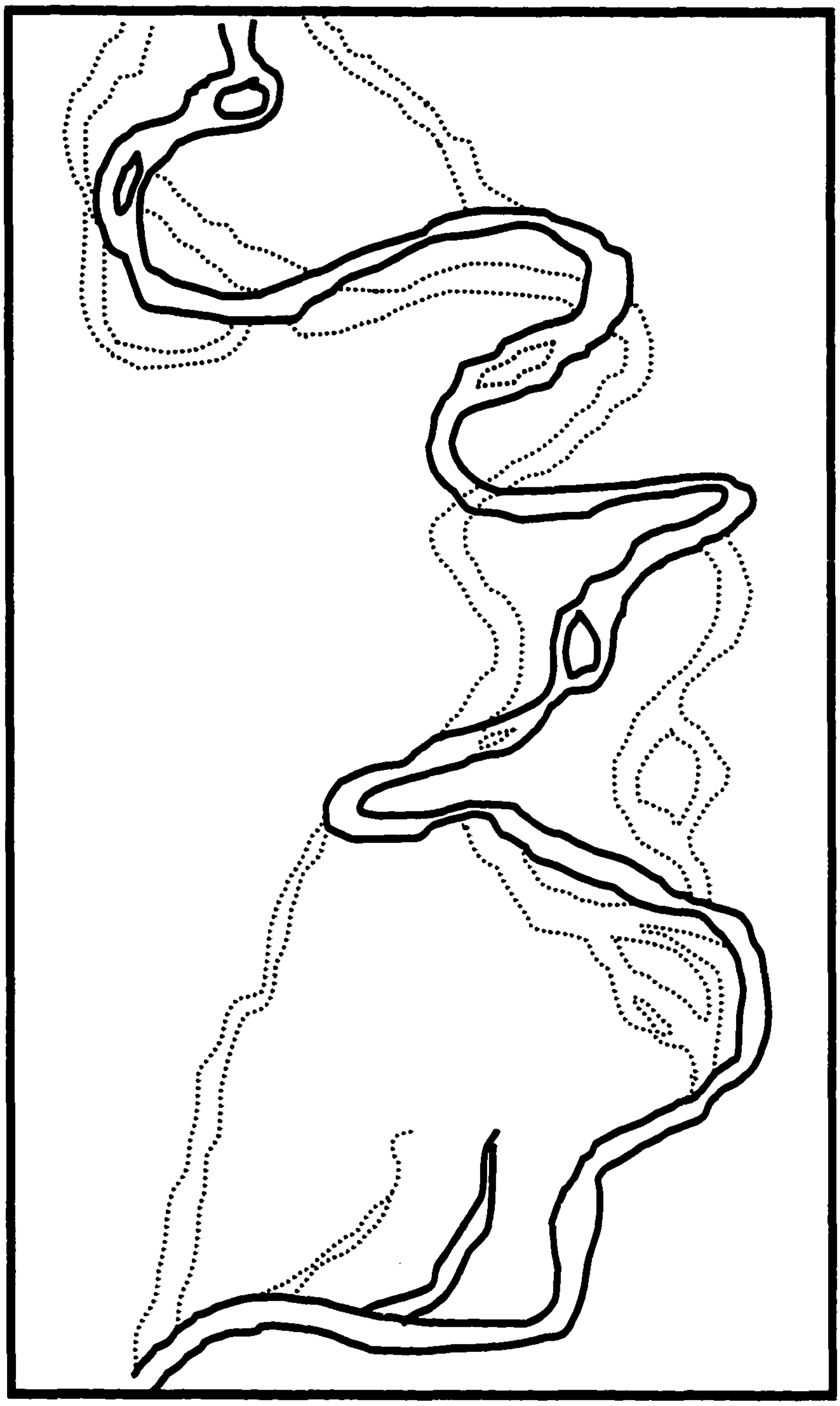

Figure 2. Example of a large braided or anastomosed alluvial floodplain. Seasonal channels and surfaces shown as dashed lines. Those channels without upstream surface connection illustrate springbrooks. Direction of flow is from top to bottom.

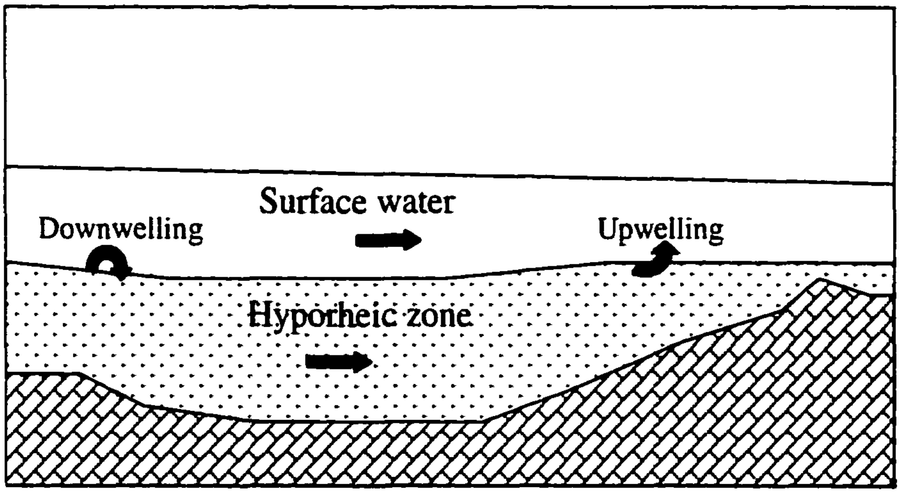

Figure 3. Diagram illustrating vertical gradients in hyporheic exchange and flow of stream and ground water in channel and through sediment interstices.

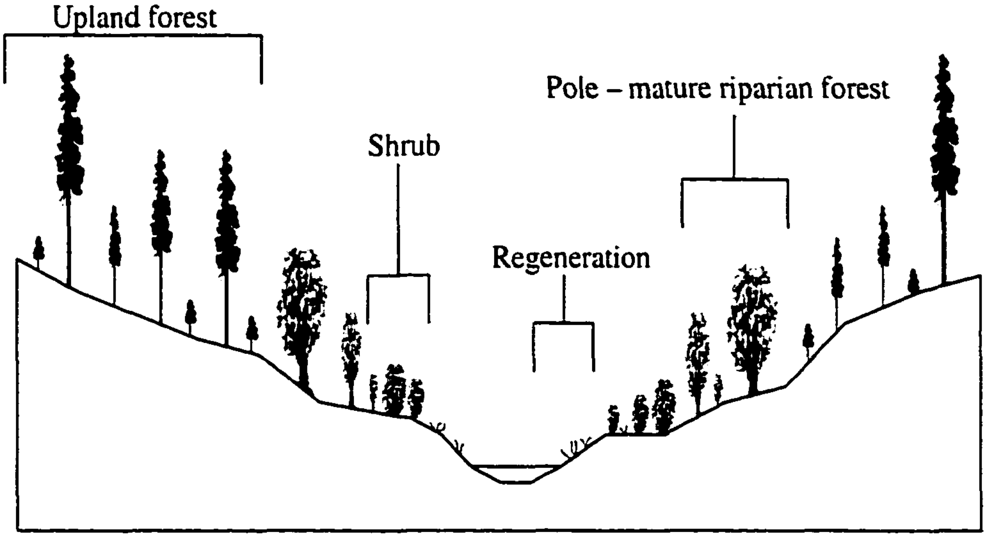

Figure 4. Simplified diagram illustrating common conceptualization of vegetation zonation in response to a continuous disturbance gradient.

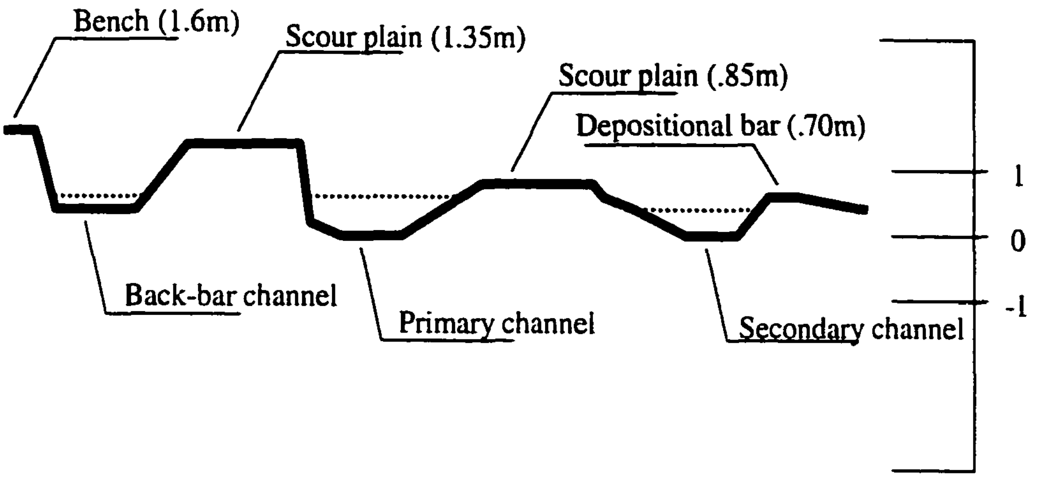

Figure 5a. A cross section on the Talkeetna River, Alaska, illustrating actual Elevational profile of habitats and channel types present. Note the inconsistent vertical positioning of habitats. Lateral distances are not to scale. (from chapter 2)

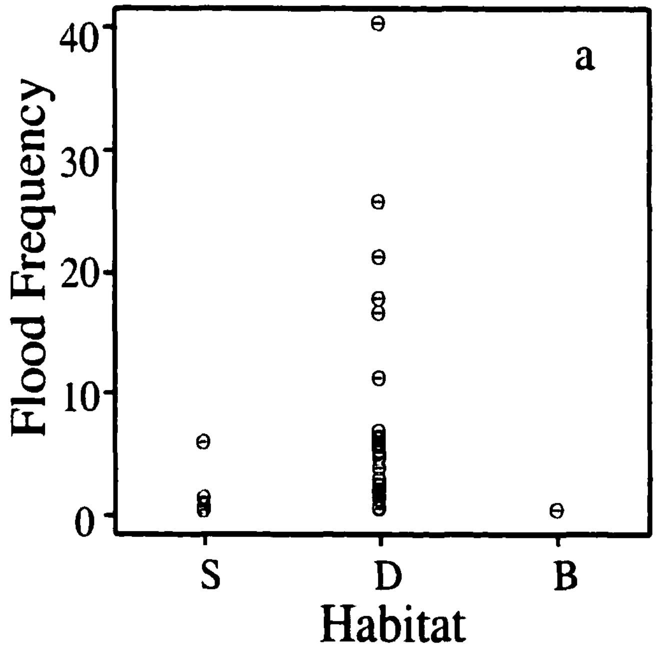

Figure 5b. Habitats (S = scour plains, D = depositional bars, and B = floodplain bench) on the Talkeetna River vs. their flooding frequency (from chapter 2).

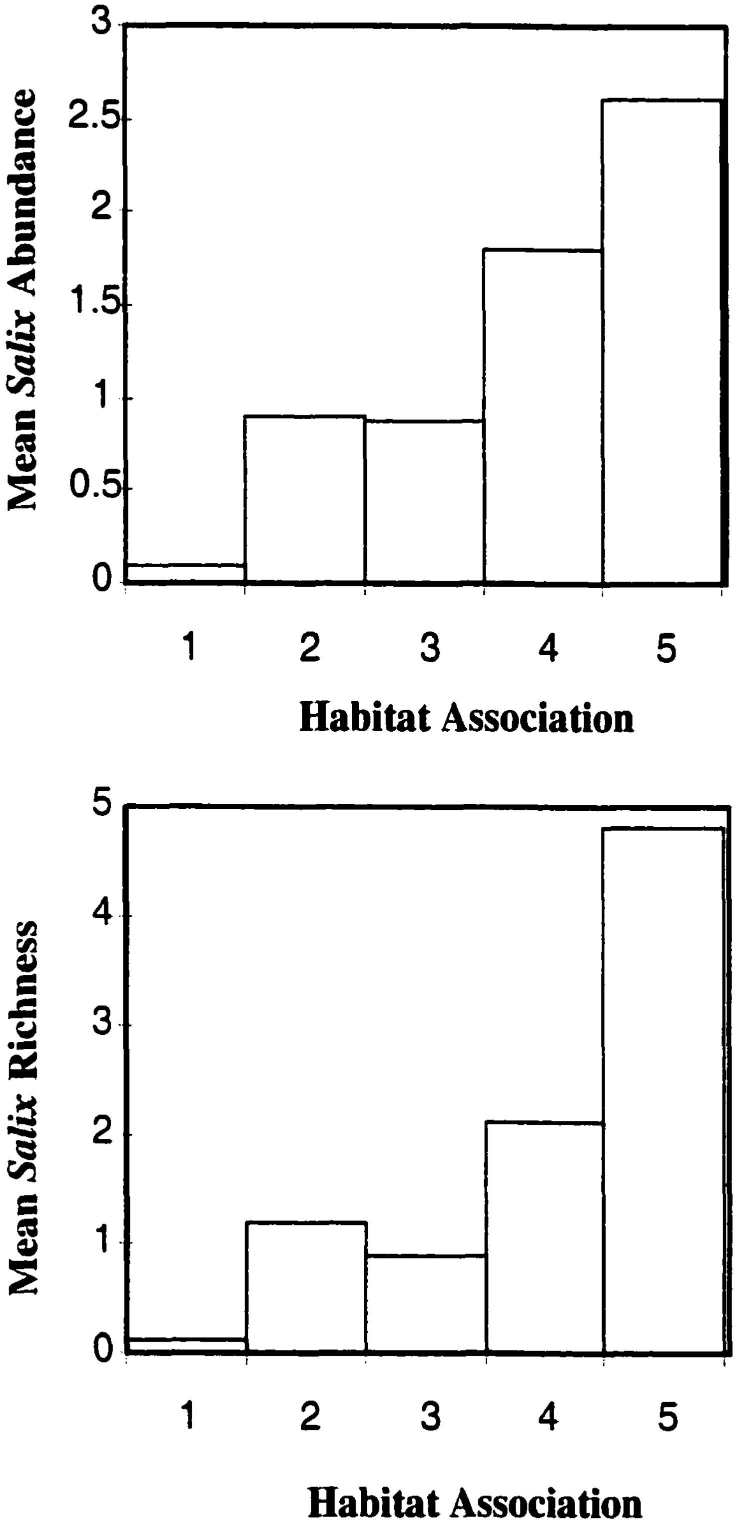

Figure 6. Data from the Middle Fork Flathead River (see Mouw 2000). (a) Mean *Salix* abundance, (b) mean *Salix* richness by habitat association (1 = scour plain, 2 = depositional bar, 3 = bench, 4 = springbrook, and 5 = backflow).

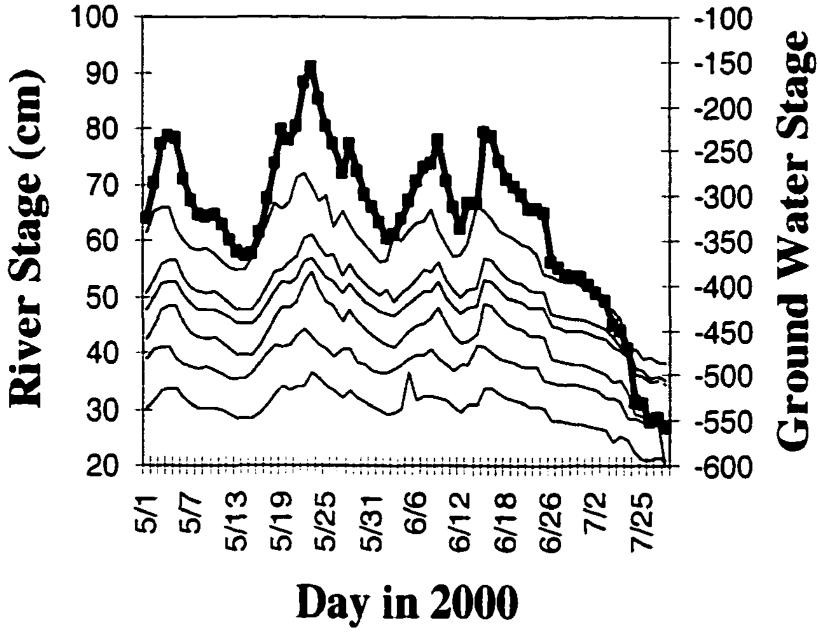

Figure 7. Line graph showing connectivity between groundwater and surface water (dark line). Stages are not relative to one another (from Chapter 2).

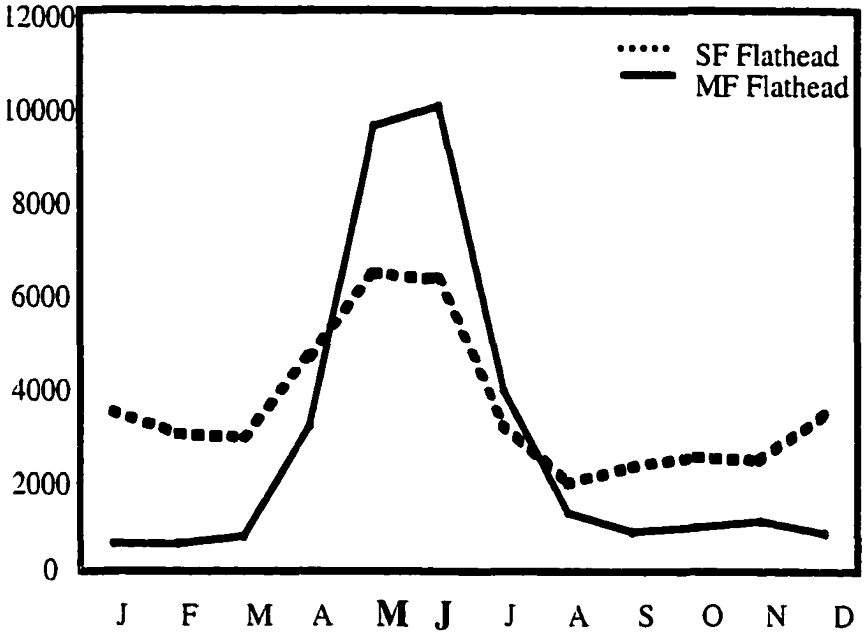

Figure 8. Discharge of the South Fork Flathead below Hungry Horse Dam, and the unregulated Middle Fork Flathead at West Glacier, Montana with 71 and 64 years of continuous record, respectively. *Salicaceae* seed dispersal is typically within the months May and June (in bold) in this region. Note the differences in pattern between the two hydrographs. For the South Fork, the annual peak is displaced in time. Peak discharge is also reduced, which typically exceeded 10,000 cfs in June prior to regulation. (derived from US Geological Survey data).

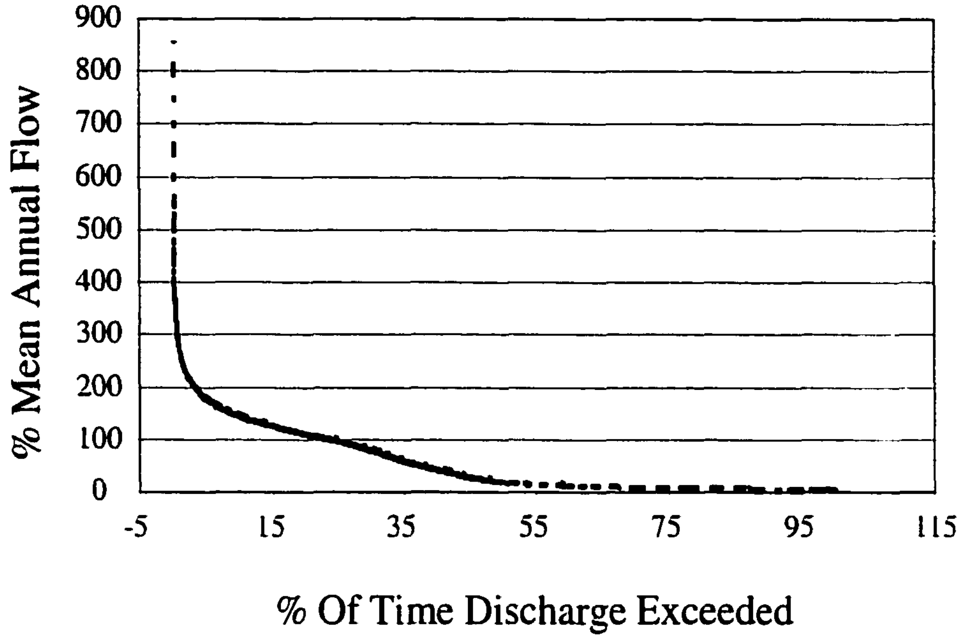

Figure 9. Flow duration curve developed for the Talkeetna River from the period of record (1964-2000, USGS station # 125719).

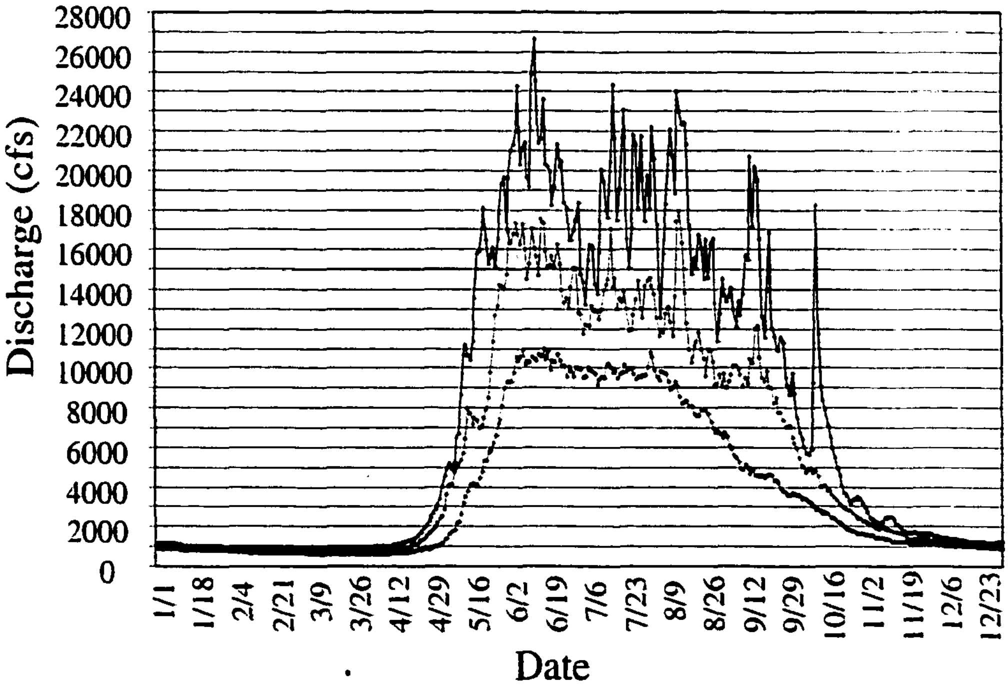

Figure 10. 50th, 85th, and 90th percentile flow lines for the Talkeetna River, Alaska. (derived from US Geological Survey data, station # 15292700).