Fragmentation Of Riparian Floras In Rivers With Multiple Dams

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Abstract. Rivers are increasingly fragmented by dams, resulting in disruption of natural dispersal pathways and subsequent changes of riverine communities. We assessed the effect of dams as barriers to plant dispersal along rivers by comparing the flora of vascular plants between pairs of run-of-river impoundments in northern Sweden. Adjacent impoundments in similar environmental settings develop different riparian floras because species with poor floating capacity become unevenly distributed among impoundments. Such discontinuities were not found along a free-flowing river, suggesting effective dispersal of riparian plants in the absence of dams. Given that dams regulate most of the world's rivers, floristic disruptions of riparian corridors may be a global phenomenon. The extensive fragmentation of other ecosystems may have caused similar obstructions to organism dispersal, with subsequent changes in species composition.

Key words: corridor functions; dams as barriers to plant dispersal; dams vs. ecological riparian continuity; fragmentation; hydrochory; plant species composition and dispersal; regulated rivers; riparian vegetation; seed dispersal; Sweden; vegetative dispersal.

INTRODUCTION

Riparian zones are among the most diverse, dynamic, and complex habitats on the world's continents (Naiman and D[acute{e}]camps 1997). Rivers and their adjoining riparian zones are considered to be the most important corridors for movements of animals in natural landscapes (Forman and Godron 1986, Malanson 1993). Natural riparian zones are also effective pathways for plant dispersal: the rivers carry large numbers of plant diaspores over long distances (Schneider and Sharitz 1988, Nilsson et al. 1991b, Johansson and Nilsson 1993), and riparian zones are rich in water-dispersed plants (Johansson et al. 1996) and rapidly spreading exotics (Planty-Tabacchi et al. 1996). Rivers are increasingly fragmented by dams (Dynesius and Nilsson 1994), potentially disrupting natural dispersal pathways and causing changes in riverine communities (Hanson et al. 1990, Zwick 1992, Fahrig and Merriam 1994). Such alterations have however been documented only for migratory fish (Petts 1984).

Many rivers have been converted to stairs of lake-like water bodies interrupted by dams and underground passages. Dams are barriers to the movement of fish (Petts 1984) and waterborne vascular-plant diaspores (Nilsson et al. 1993), and regulated riparian zones harbor fewer vascular plant species than free-flowing ones (Nilsson et al. 1997). In free-flowing rivers (Fig. lA), floating diaspores are rapidly transported far downstream during floods (Nilsson et al. 1993). This effective dispersal is hypothesized to homogenize the floristic composition among riverbank sites, because any riverbank site may be colonized by species from a large portion of the river valley.

In impounded rivers (Fig. 1B), current velocity is low and floating diaspores either sink or become swept ashore by winds. A few diaspores may pass dams through turbines or spillways. Long floaters are more likely to pass, because passages are hard to hit, and long floating-times increase the probability of success. Short floaters may be absent from impoundments because they fail to recolonize after local extinction (Fahrig and Merriam 1994). Riverbanks will thus be colonized by species from other sections of the same impoundment and from surrounding uplands rather than by species from upstream areas. We hypothesize that in rivers fragmented by dams, riparian floras will become more similar among sites within an impoundment than among sites between impoundments (Fig. 1B). In contrast, in free-flowing rivers with effective dispersal, equivalent differences between adjacent slow-flowing reaches are not expected. Instead, floristic transitions are hypothesized to be gradual along the river (Fig. 1A).

STUDY AREAS

We selected 20 run-of-river impoundments in the Lule, Skellefte, Ume, and [dot{A}]ngerman Rivers in northern Sweden for study, Their main channels are regulated for hydropower by 9 to 16 dams in each river, and mean annual discharge ranges between 155 and 500 m3/s. Run-of-river impoundments are consecutive along the middle and lower main-river channels; tailwater reaches are absent or scarce. The impoundments provide water to hydropower stations, and water levels fluctuate daily or weekly between their statutory high and low levels throughout the year. Adjacent impoundments were chosen so as to minimize differences in waterlevel regime, age of regulation, and impoundment length. The selected impoundments were between 4.5 and 49 km long, separated by dams and by 0 to 6.5 km long, dry reaches of the former channel. The difference in altitude between the paired impoundments was 20 to 87 m (mean 32 m), while the altitudinal range within impoundments was none or very small. The impoundments were on average 471 m wide at the study sites. All impoundments were between 25 and 40 yr old. Water-level fluctuations during the growing season ranged between 0.35 and 1.69 m, and bank widths between 0.13 and 18.8 m.

In the free-flowing Vindel River, we selected 10 slow-flowing stretches. The Vindel River is a tributary to the Ume River with a mean annual discharge of 200 [m.sup.3]/s, and exhibits seasonal water-level fluctuations ranging up to 6 m, including spring flooding. The river is on average 425 m wide at median flow, measured at 25 points distributed along its entire length. The length of the slow-flowing stretches ranged between 5.5 and 30.0 kin, and the rapids in between were between 2.1 and 3.5 km long. Botanical surveys, photos, and remnants of preregulation vegetation, now left unflooded, confirm that, before hydroelectric exploitation, riparian vegetation was similar between the Vindel River and nearby, now-regulated rivers (Nilsson et al. 1991a). The riparian floras of the entire Vindel River and the regulated Ume River are highly similar: for 25 sites in each river, there were 257 species in the Ume River and 254 species in the Vindel River. The floristic similarity (Jaccard's index) between the floras w as 0.73.

METHODS

Site sampling

The run-of-river impoundments were grouped in 10 pairs. Each pair consisted of two adjacent impoundments with similar environmental conditions. The slow-flowing stretches in the free-flowing river were grouped in five pairs, where each pair consisted of two adjacent slow-flowing stretches separated by a stretch of rapids. In the regulated rivers, dams were built on such rapids, and the slow-flowing stretches were turned into run-of-river impoundments. Each impoundment or slow-flowing

stretch was divided into three equally long sections, with one study site in the middle of each section (Fig. 2).

In the regulated rivers, each study site spanned a 200-m-long strip between the damming and summer-drawdown levels. In the free-flowing Vindel River, we sampled a 200-m-long area between the spring-flood high and summer low levels. At each site we recorded the presence of all vascular plant species, the width and height of the riverbank, substrate fineness, substrate heterogeneity, and the disturbance from wave action. We measured bank width as the horizontal distance between the highest and lowest water levels attained during the growing season. Bank height was measured as the vertical distance between these two levels, using a rod and level. We determined percentage cover of substrate types by classifying according to particle size into peat, clay, silt, sand, gravel, pebbles, cobbles, boulders, and bedrock. Substrate fineness was calculated by weighing [log.sub.2]-transformed values of mean particle size by percentage composition of the riverbank substrate, and substrate heterogeneity was calculated as th e number of substrate types per site. Wave disturbance was estimated by measuring the fetch for wave height on maps as the width of the river perpendicular to the center of the riverbank site. The definition of a species follows Krok and Almquist (1994) except that Alchemilla spp., Hieracium spp., Rhinanthus groenlandicus R. minor, Sparganium spp., Sagittaria spp. and Taraxacum spp. were treated as one taxon each. We sampled the sites along the regulated rivers in 1995 and the free-flowing sites in 1997.

Data analysis

To test for fragmentation of riparian floras, we compared the floristic similarity (Jaccard's index) between all sites in two adjacent impoundments by using the means of all possible pairwise combinations (Fig. 2) within and between these two impoundments using a paired-samples t test.

To control for any effect of unequal distances between sites, we regressed floristic similarity on distance between sites, and used the residuals to test if sites were still more similar within than between impoundments.

Plant species composition could differ because of environmental differences among impoundments. We examined this by calculating differences between all sites of a pair for all measured environmental variables known to affect species composition, i.e., bank width and height, substrate fineness and heterogeneity, and wave disturbance (Keddy 1983, Nilsson et al. 1989, Nilsson et al. 1991a). Then we tested whether differences were smaller within than between impoundments.

Even if differences for each environmental variable were not statistically significant, small differences in many variables may explain dissimilarities in flora between impoundments. Therefore, we performed a correspondence analysis (CA; ter Braak 1990) and removed all variation in species composition that could be attributed to environmental variables by regressing the first CA axis on the environmental variables. Then we tested whether the residuals had higher positive values within than between impoundments.

To evaluate whether any observed floristic dissimilarity between impoundments was associated with the dams, or represented remnants of preregulation differences, we repeated the above comparisons in a free-flowing river. We compared adjacent slow-flowing stretches using the same methodology as in the impoundments (Fig. 2). Analysis of statistical power showed that five pairs of slow-flowing stretches were enough to detect a difference similar to that found in the regulated rivers. The power analysis was made using PASS 6.0 (Number Cruncher Statistical Systems; J. L. Hintze, Kaysville, Utah, USA).

To test for dispersal-dependent differences among species in their response to fragmentation, we classified species according to dispersal by wind, vertebrates (epizoic or endozoic), ants, or if they lack any special mechanisms for dispersal (Willson et al. 1990). Water dispersal and vegetative dispersal complemented this classification. Species with seeds and fruits that float for [geq]2 d were defined as "long floaters"; the remaining species were "short floaters" (Romell 1938, Danvind and Nilsson 1997). Species with differentiated vegetative structures that can be detached and dispersed were defined as capable of vegetative dispersal. All classifications included the entire flora, except for floating ability where data were available for 155 of 262 species (105 long floaters and 50 short floaters). We identified species for which dams may be barriers by counting species having at least two more occurrences (out of three possible, Fig. 2) in one impoundment of a pair. We then tested for differences in disp ersal strategy (i.e., dispersal by water, wind, vertebrates [epizoic or endozoic], or ants, vegetative dispersal, and species without any special mechanisms for dispersal), between these species and the remaining ones.

RESULTS AND DISCUSSION

Floristic similarity (Jaccard's index) between sites was significantly higher within than between impoundments (Table 1). This was not an effect of unequal distances among sites, because the residuals had higher positive values within than between impoundments (within: 0.019 [pm] 0.011 [mean [pm] 1 SE], between:-0.002 [pm] 0.012, P = 0.0023, one-tailed paired-samples t test). We found no statistically significant difference between impoundments for any of the environmental variables (P [greater than] 0.05, paired-samples t tests). Furthermore, the residuals from regressing the correspondence-analysis axis on the environmental variables were still more similar within than between impoundments (within: 26.4 [pm] 3.55 [mean [pm] 1 SE], between: 38.0 [pm] 3.71, P = 0.024, one-tailed paired-samples t test), suggesting that the floristic dissimilarity between impoundments was not due to environmental differences but to dispersal limitation caused by dams.

Floristic similarity (Jaccard's index) between sites did not differ significantly within and between slow-flowing stretches in the free-flowing Vindel River (Table 1), suggesting that plant dispersal along the river is not limiting species composition. This may be because regular events of long-distance dispersal maintain sink populations along the free-flowing river, and a specific riverbank site may be colonized by species from a large source area. We cannot rule out the possibility that the floristic dissimilarity among impoundments was due to an unmeasured environmental variable rather than to barrier effects of dams. If so, that variable should relate to regulation measures, because free-flowing stretches did not differ floristically (Table 1). However, this is unlikely considering that we selected pairs of impoundments to avoid differences in regulation measures.

Species with short-floating diaspores (floating [less than]2 d) were overrepresented among species with at least two more occurrences in one impoundment of a pair (P = 0.0055, [[chi].sup.2]-test, exact two-tailed significance), but no other mechanism for dispersal was significantly more common in either group (P [geq] 0.19). This supports the prediction that dams are barriers primarily to species with poor floating ability.

The difference in floristic similarity within and between impoundments may not seem impressive (Table 1), but species presence/absence data are a crude measure of barrier effects. First, it might be that a species is present on both sides of a dam, yet without any dispersal across it. Second, plants from upland areas may also invade riparian zones, and widespread species are likely to colonize several impoundments without passing the dams. Therefore, our study only quantifies minimum effects. Despite this, it supports the hypothesis that dams act as barriers to plant dispersal and that individual

impoundments develop different riparian floras. These floristic dissimilarities are likely to remain, because all impoundments were 25-40 yr old, when postregulation diversity has stabilized (Nilsson et al. 1997).

The implications of this study are clear: First, ecological continuity (Vannote et al. 1980) in regulated rivers is lost not only for the river channel (Ward and Stanford 1983), but also for the adjoining riparian corridor. Considering that riparian corridors have central ecological functions in landscapes (Naiman and Décamps 1997), the results indicate that dams may have landscape-level effects that are difficult to predict. Second, many of the hypotheses on corridor function remain untested, despite wide application in conservation biology (Hobbs 1992, Smith and Hellmund 1993). For example, stream corridors are commonly used in reconnecting remnants of natural habitats (Bueno et al. 1995), but such corridors are often highly fragmented and disturbed, calling in question their function as conduits for dispersal. These issues should be considered in future dam-relicensing and river-rehabilitation schemes, so that ecological and socio-economic benefits are optimized (Naiman 1992). Third, the extensiv e fragmentation of other ecosystems may have caused similar obstructions to organism dispersal, with subsequent changes in species composition (Tilman 1997).

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