Substratum stability associated with the riverine macrophyte *Justicia americana*

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SUMMARY

1. Patches of stable substratum in streams may be important refugia for benthic organisms during scouring floods. Streambed stone stability, packing and embeddedness were assessed within and adjacent to beds of the macrophyte *Justicia americana* in five Alabama streams.
2. The force needed to dislodge stones and embeddedness was about two times lower outside *Justicia* beds than within them. Significant positive correlations between stone stability and (i) degree of embeddedness, and (ii) the abundance of binding rhizomes and the presence of attached roots indicate that *Justicia* may physically modify the local streambed, indirectly enhancing substratum stability and reducing flow, thereby increasing sand deposition.
3. Despite higher stability (i.e. physical refugia during bed-moving spates) within *Justicia* beds, the abundance of epilithic plants (moss and *Podostemum ceratophyllum*) and pleurocerid snails (*Elimia* spp.) was similar both inside and outside the macrophyte beds. Several physical characteristics within macrophyte beds, such as low light, reduced current and increased sand intrusion, may create suboptimal conditions for benthic organisms in these habitats.
4. Additional work is needed to determine if *Justicia* biogenically enhances substratum stability or if its presence merely reflects patches of stable substratum within the streambed. Regardless of the mechanism, there is an association between *Justicia* beds and streambed characteristics.

Keywords: critical force, disturbance, *Justicia americana*, macrophyte, substratum stability

Introduction

Disturbance plays an important role in regulating populations, community interactions and ecosystem processes in streams (Resh *et al.*, 1988; Reice, 1994). Floods, in particular, can re-shape channels, scour streambed material and displace organisms. The persistence of benthic organisms in unstable, flood-prone streams has been attributed to traits that enhance resilience and/or resistance, including life history [e.g. rapid development, mulivoltinism (Scrimgeour & Winterbourn, 1989)], immigration (Gray, 1981) and behaviour (Graesser, 1987; Lytle, 1999). Stream communities can recover within the lifetime of most taxa (several weeks to months) following apparently devastating floods (e.g. Scrimgeour, Davidson & Davidson, 1988; Angradi, 1997), so investigators have begun to examine the importance of physical refugia as a mechanism underlying rapid recovery. Organisms inhabiting refugia, such as interstitial spaces within subsurface sediments, amongst large embedded stones, woody debris, and within areas of permanently low shear stress, or the adjacent floodplain, have been considered important sources for recolonising populations following disturbance (Lancaster & Hildrew, 1993; Golladay & Hax, 1995; Bergey, 1999). For example, Cobb, Galloway &

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Flannagan (1992) found that benthic insect densities were negatively correlated with discharge and substratum particle movement in a Canadian stream, indicating that patch-specific stability of in-stream substrata may be sufficient to reduce the impact of floods. Substratum stability may be even more critical for sessile organisms, such as bryophytes, because of their slow recolonisation rates. For example, the abundance of bryophyte cover was higher in reaches of 58 New Zealand streams with coarser substrata than in those dominated by smaller stones (Suren & Duncan, 1999).

Many factors contribute to the patchy nature of stone movement during floods (Downes *et al.*, 1998; Matthaei, Peacock & Townsend, 1999). Critical shear stress (τ_c = tractive force) is the mechanical force per unit area required to move a stone downstream. In addition to stone size, critical shear stress also depends upon stone shape, density and spatial arrangement (Gordon, McMahon & Finlayson, 1992). Larger scale factors also determine stone entrainment during high-flow events. The bulk of bedload movement occurs on sloping streambeds (surfaces of gravel bars), where depth is intermediate between the deepest part of the channel (thalweg) and the stream margin (Leopold, 1994). Similarly, channel morphology also influences substratum stability, with stones in narrow, constrained channels being less stable than those in reaches with wide floodplains. Rooted aquatic plants (macrophytes) stabilise and reduce resuspension of littoral sediments in lakes (James & Barko, 1990; Petticrew & Kahlff, 1992) and coastal marine habitats (e.g. Orth, 1977; Bruno & Kennedy, 2000), but their role in stabilising substrata within streams has not been tested empirically.

Justicia americana L. (Vahl.) (water-willow, hereafter called *Justicia* is an emergent macrophyte common to eastern piedmont streams of North America. Its geographic range extends from Quebec to Georgia where it occurs on submerged streambeds, shores and gravel bars of streams (Penfound, 1940; Radford, Ahles & Bell, 1968). There is little detailed information about the spatial coverage of *Justicia* within North American streams. However, *Justicia* appears to be limited by riparian shading in upstream tributaries and the distance between *Justicia* beds increases as shallow zones of large rivers become more interspersed (K.M. Fritz, personal observation). *Justicia* is a colonial plant that is adapted to natural flow fluctua-

tions by having a deep rhizomatous growth form, capable of vegetative reproduction if stems or rhizomes are mechanically fragmented (Penfound, 1940; Lewis, 1980). Flexible, erect stems with well-developed fibro-vascular and aerenchymous systems (Penfound, 1940) enable *Justicia* to propagate and persist in stream systems where scouring floods are common (Halsam, 1978).

Like most emergent aquatic plants, *Justicia* is highly productive and contributes much rapidly-processed coarse particulate organic matter to streams during late summer and early autumn (September to November), a time when other sources of organic matter, such as algae and deciduous leaf inputs, are scarce (Boyd, 1969; Hill & Webster, 1983). However, despite its widespread occurrence and local abundance, little is known about the biology of *Justicia* and its potential role in modifying the benthic habitat in streams.

The main objectives of this study were to determine (i) if substratum stability differed between streambed patches within *Justicia* beds and adjacent patches outside, and (ii) if the distribution of sessile and mobile organisms was associated with *Justicia* and the observed stability patterns of stones. We predicted that substratum stability would be greater within *Justicia* beds, and that the abundance of benthic organisms would be higher within *Justicia* beds where streambed disturbance would be reduced.

Methods

Study sites

We studied moderate-sized (third to fourth order) streams within the Piedmont physiographic province, where extensive beds of *Justicia* often occur (Fig. 1). Streams were tributaries within the three major drainages: Coosa River (Terrapin, Shoal and Talladega creeks), Tallapoosa River (Choctafaula Creek), and Chattahoochee River (Halawakee Creek) within east-central Alabama. Geology in the area was predominately bedrock and unconsolidated substrata consisting of phyllite and metasiltstone. Stream water was circumneutral (pH: 6.3–7.9) with low-moderate levels of dissolved ions (specific conductance: 19–189 μS cm^{-1}, 25). Channels (wetted width range from 4.2–22.1 m during summer baseflow) were moderately shaded (32–86%), with shade decreasing with increasing stream width. *Justicia* beds typically
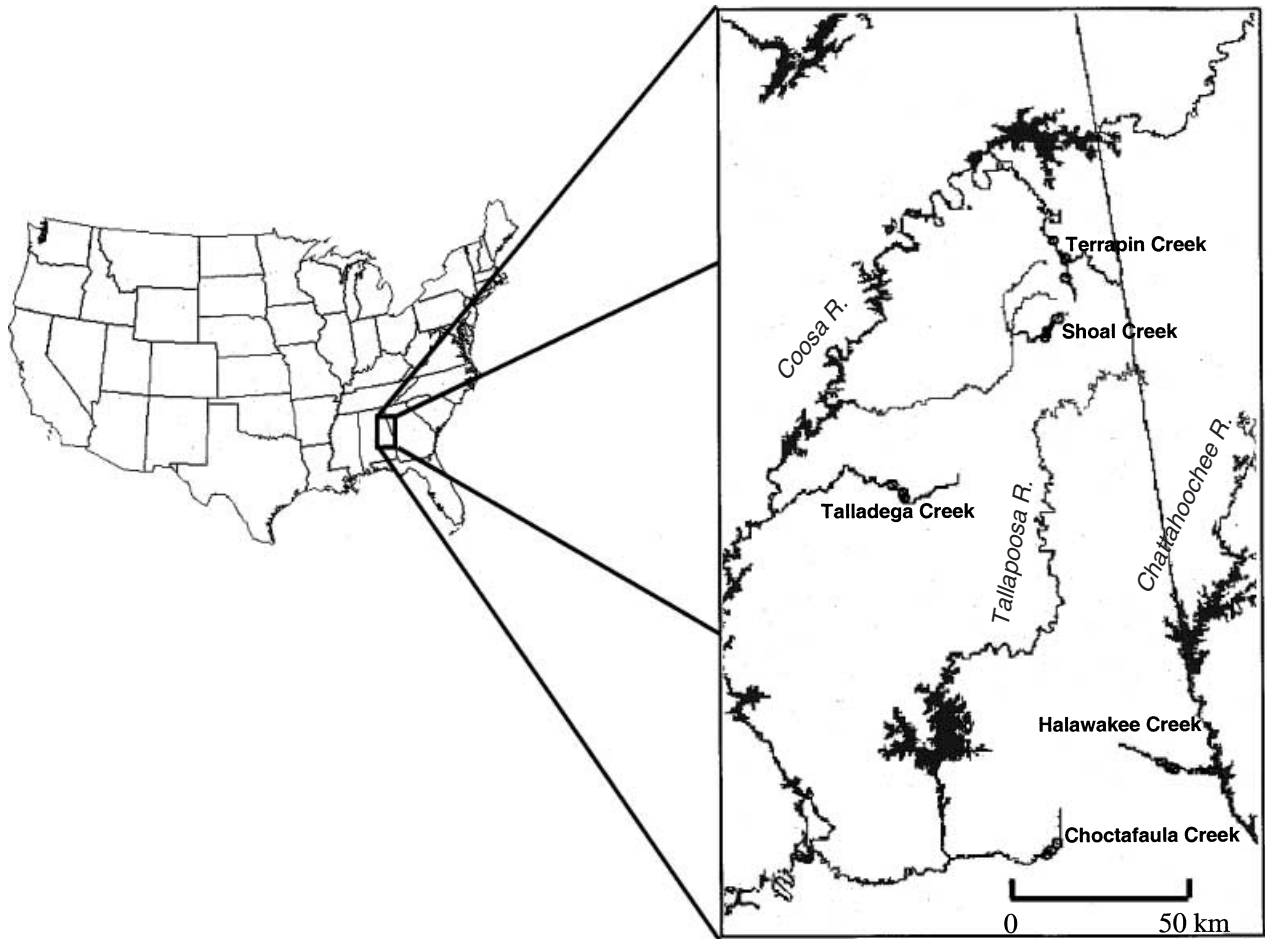
Fig. 1 Map showing location of the five study streams within east-central Alabama, USA. Circles identify location of riffles within each study stream.

occurred as continuous patches (10–100 m²) in riffles and covered 20–75% of the riffle wetted area. The area of *Justicia* beds generally increased with stream width. *Justicia* was also found as small patches (<1 m²) along sunny margins of pools and in steep, boulder dominated reaches in our study streams, but these patch-types were infrequent. Mixed deciduous (e.g. *Liquidambar styraciflua* L., *Liriodendron tulipifera* L., *Acer* spp., and *Quercus* spp.) and conifer (primarily *Pinus taeda* L.) forest dominated riparian zone and uplands, respectively, for all the streams. The study took place during the summer baseflow period (July–August 2000).

Study design

We used a nested design where *Justicia* beds within three riffles were nested within each of the five

streams. Three transects (*ca.* 1 m wide) within each riffle were randomly selected across the channel, encompassing areas within and outside of a *Justicia* bed. Twenty focal stones (top surface ≥40 mm maximum dimension perpendicular to the flow) were randomly selected per transect with 10 stones within and 10 stones outside of *Justicia* beds. A total of 900 stones across 15 riffles and 45 transects were measured for the five streams.

Abiotic measures

Substratum stability was measured by quantifying the force required to shift stones at rest from the streambed (Sousa, 1979). Force was measured with a spring balance (Homs tubular scales) attached to a pair of curved grappling hooks (see Downes, Glaister & Lake, 1997 for method). Balances were pre-calibrated for the

mass of the grappling hook (measurable ranges of 0.05–5, 0.1–10, and 0.25–25 kg, for small, medium and large stones, respectively). In use, the grappling hook tips were placed in contact with the upstream edge of a focal stone. One of the three spring balances was then attached between the hooks, pulled parallel to the streambed (so that the angle between the spring balance and the vertical axis of the focal stone was *ca.* 90) and in the direction of flow. The mass required to shift the stone 5 cm was recorded and then used to calculate Newtons of force [product of mass and acceleration because of gravity (9.807 m s^{-2}0), critical force, F_C *sensu* Downes *et al.*, 1997]. Although there are limitations to this method (e.g. angles to which natural shear forces act on stones are likely to vary across time and space), this measure is believed to provide a better estimate of force required to move stones, compared with equations developed in flumes that predict stone movement during a given magnitude or frequency of flood (see Downes *et al.*, 1997; Matthaei *et al.*, 1999).

After locating focal stones, but before measuring F_C, water depth was measured and degree of stone wedging was assigned (values of 0–3 corresponding to 0, 1–33, 34–66, and 67–100% of stone surface area touching larger adjacent stones). If a stone could not be moved within measurable limits of the spring scales, another stone was randomly selected along the transect (this only occurred for four stones over the entire study). After F_C was measured, we assigned the stone to one of five categories of embeddedness (0, 1–25, 25–50, 50–75 and 75–100% of the stone surface area surrounded by smaller particles, predominately sand), scored visually by the contrasting surface colouration of the portion of a stone exposed to the current compared with the portion of stone surface area surrounded by sediments. Unembedded stone surfaces in Piedmont streams are typically darker than embedded surfaces (because of manganese oxide deposits and organic staining, B.G. Lockaby, personal communication).

Additional factors measured included stone size (length, height and width), *Justicia* stem density (within 0.125 m^2 circular area around focal stones), current velocity (Marsh-McBirney Flo-Mate), and the relative distance of selected stones from channel wetted-edge and thalweg. Because wetted width varied among transects, riffles and streams a relative or proportional measures of position (distance of a stone to the nearest bank or thalweg divided by total wetted width along a transect) within the channel was used to assess the role of channel position on the various dependent variables. The number of *Justicia* rhizomes binding stones and the presence of attached roots to stones also were recorded for a subset of riffles within Terrapin and Talladega creeks.

Benthic organisms

To determine the potential influence of *Justicia* on other stream organisms we chose two abundant and ubiquitous groups of benthic organisms which contrasted strongly in their mobility and trophic state: (i) mobile snails within the family Pleuroceridae (primarily *Elimia*), and (ii) two groups of epilithic plants, moss (primarily *Fontinalis*) and *Podostemum ceratophyllum* Michx. (riverweed). *Elimia* is known to be a competitively dominant grazer within small streams of Eastern North America, and is often the largest contributor (>90%) to total invertebrate biomass (Newbold *et al.*, 1983). Pleurocerid snails track periphyton abundance (Hill, Boston & Steinman, 1992) and use flow refugia in laboratory streams (DeNicola & McIntire, 1991). Moss and *Podostemum* (hereafter called epilithic plants) require attachment to stable stones, but have different optima for light and water depth. *Podostemum* dominates in deep, fast flowing and open locations, whereas, *Fontinalis* dominates more shallow and shaded locations (Everitt & Burkholder, 1991; Munch, 1993).

All snails visible were detached and counted prior to measuring F_C for focal stones. After F_C was measured, the stone was searched again and any further snails counted. Epilithic plant abundance was quantified by assigning stones to one of five categories of percent cover (0, 1–25, 25–50, 50–75 and 75–100% of stone surface area covered).

Statistical analyses

Variation in F_C, stone embeddedness, wedging, size, snail abundance and % epilithic plant cover was examined using nested ANOVA (PROC GLM, SAS, 2001) with streams, riffles and the presence or absence of *Justicia* as main factors. The statistical model used included *Justicia* presence/absence (fixed factor) nested within riffles, and riffles nested within streams. Our objective was to compare variation in stone

stability within and outside *Justicia* beds rather than among streams and riffles, so we averaged values across each treatment within a transect, resulting in 45 replicates per *Justicia* treatment across the five streams. Averaging across transects normalised categorical data (e.g. embeddedness, wedged) and thus met the assumptions of parametric analyses. Continuous data were log-transformed where assumptions of normal distribution or heterogeneous variances were not met (Shapio-Wilk Test for normality and residual plots for equality of variance; Zar, 1984).

We explored possible explanations for differences in stability and the abundance of organisms on stones within and outside *Justicia* beds by the strength of association between habitat measures and organism abundance. Associations were tested using the partial correlation coefficients among variables, measured using multivariate analysis of variance (MANOVA, PROC GLM, SAS, 2001). A separate MANOVA included only data for stones within *Justicia* beds to investigate the associations among streambed characteristics measured and those unique to stones within *Justicia* beds (rhizome abundance and presence/absence of attached roots). A three-level nested model (i.e. stream, riffle and transect) was used in this analysis rather than pooling stones within transects. Significance level was set at $\alpha = 0.05$ for all statistical analyses.

Results

The force ($\mathbf{F}_C$) needed to move stones differed significantly across all three hierarchical levels (streams, riffles, and within versus outside *Justicia* beds; Table 1). Among streams, stones within *Justicia* beds required a significantly greater force than stones adjacent to *Justicia* beds (Fig. 2a). In most streams mean $\mathbf{F}_C$ required to move stones within *Justicia* beds was two times greater than for stones outside *Justicia* beds. Stones within *Justicia* beds also had a higher degree of embeddedness than those outside beds, but embeddedness did not differ significantly among streams or riffles (Table 1). On average >50% of the surface area of stones from *Justica* beds was embedded in sand, whereas stones outside of *Justicia* were only *ca.* 25% embedded (Fig. 2b). Stone size (α-axis) differed significantly among streams and riffles (Table 1), but did not differ within and outside *Justicia* (Fig. 2c; Table 1). Similarly, the intermediate and

Table 1 Nested analyses of variance results for the force ($\mathbf{F}_C$) needed to move stones, stone size (α-axis length or the longest dimension), degree of stone embeddedness, degree of stone wedging, number of *Elimia* per stone, and percent cover by epilithic moss and *Podostemum ceratophyllum*. *Justicia* refers to riffle areas within (versus outside) *Justicia* beds

Source of variation	SS	d.f.	MS	F	P
$\mathbf{F}_C$†					
Stream	1.80	4	0.45	9.28	<0.0001
Riffle	2.98	10	0.30	6.14	<0.0001
Justicia	8.03	1	8.03	165.62	<0.0001
Full model	12.81	15	0.85	17.61	<0.0001
Stone size†					
Stream	0.09	4	0.02	5.86	0.0004
Riffle	0.20	10	0.02	4.92	<0.0001
Justicia	0.002	1	0.002	0.73	0.39
Full model	0.26	15	0.02	4.89	<0.0001
Embeddedness					
Stream	1.03	4	0.26	0.78	0.54
Riffle	5.87	10	0.59	1.77	0.08
Justicia	38.02	1	38.02	114.73	<0.0001
Full model	44.92	15	2.99	9.04	<0.0001
Wedging					
Stream	0.44	4	0.11	1.69	0.16
Riffle	0.95	10	0.09	1.45	0.18
Justicia	0.08	1	0.08	1.15	0.29
Full model	1.47	15	0.10	1.49	0.13
Elimia					
Stream	226.70	4	56.67	23.45	<0.0001
Riffle	85.84	10	8.58	3.55	0.0007
Justicia	18.14	1	18.14	7.5	0.008
Full model	330.67	15	22.04	9.12	<0.0001
Epilithic plants					
Stream	2.73	4	0.68	2.79	0.03
Riffle	10.40	10	1.04	4.26	<0.0001
Justicia	0.37	1	0.37	1.53	0.22
Full model	13.50	15	0.90	3.69	<0.0001

†Log-transformed before analysis.

shortest axes of stones did not differ significantly between locations within riffles ($P > 0.05$). The degree of stone wedging did not differ significantly across the hierarchical levels tested (Table 1).

The abundance of *Elimia* on stones varied significantly across the three hierarchical levels ($P < 0.0001$; Table 1). In contrast to our prediction, snails were more abundant on stones outside *Justicia* beds, indicating that snail distribution was inversely related to stone stability. Separate analyses for each stream revealed that *Elimia* abundance was significantly higher on stones outside of *Justicia* in Shoal Creek (ANOVA, $F_{1,16} = 6.76$, $P = 0.0194$), but did not differ between stones within or outside of *Justicia* beds in the other four streams (Fig. 3a). Epilithic plant cover on
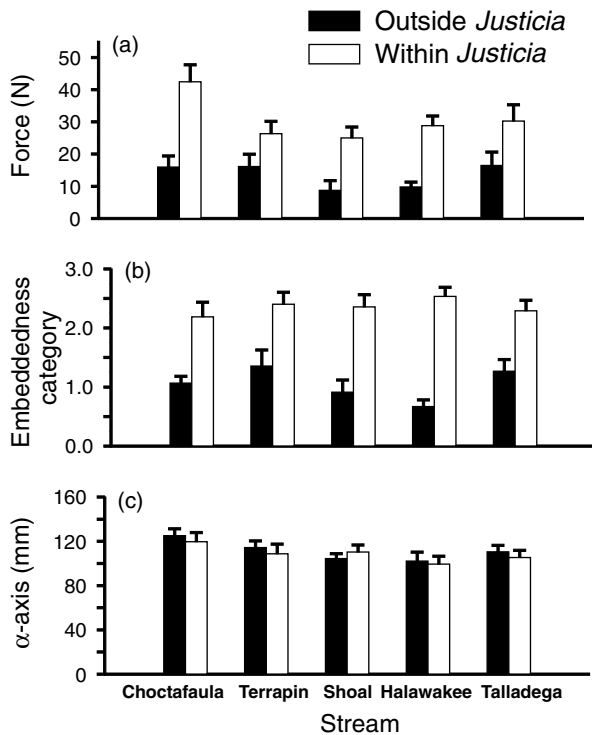
Fig. 2 Force, embeddedness category and stone size among the five study streams within and adjacent to *Justicia* beds ($\bar{X} \pm 1$ SE, $n = 9$); (a) F_C (Newtons); (b) embeddedness category (see Methods for details); (c) stone size (α-axis, mm).

Fig. 3 *Elimia* spp. (Pleuroceridae: Gastropoda) abundance and percent cover of epilithic plants (mosses and *Podostemum cerato-phyllum*) across the five study streams within and adjacent to *Justicia* beds ($\bar{X} \pm 1$ SE, $n = 9$); (a) *Elimia* (number per stone); (b) epilithic plant cover (see Methods for details).

stones differed significantly among streams and riffles ($P < 0.0001$), but did not differ between stones within or outside *Justicia* beds (Table 1; Fig. 3b).

The force (F_C) to move stones was significantly correlated with degree of embeddedness, stone size and water depth (Table 2). The abundance of *Elimia* and epilithic plant cover both increased with stone size; *Elimia* abundance also was positively correlated with epilithic plant cover. In turn, epilithic plant cover declined with increasing embeddedness, but was positively correlated with current velocity.
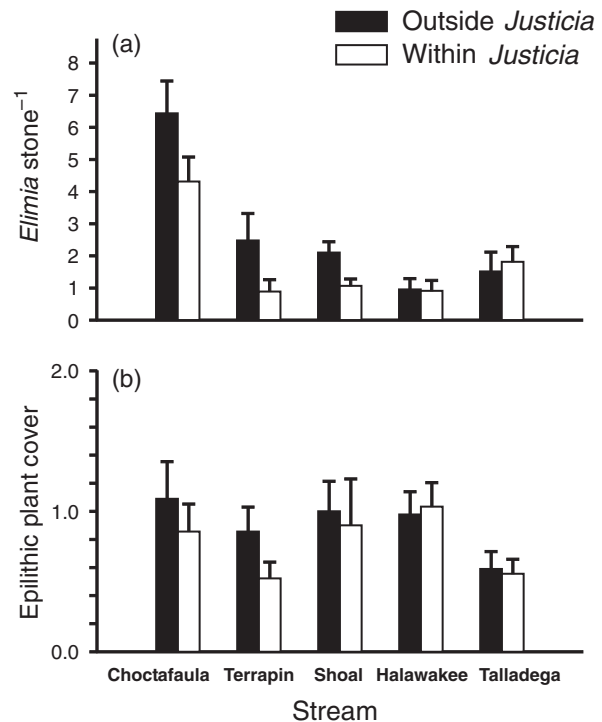
For stones within *Justicia* beds, the F_C to move stones was positively correlated with the number of intersecting rhizomes and the presence of attached roots in the stream bed. However, these variables are unlikely to be independently related to F_C, because of significant positive relationships (multicollinearity) among embeddedness, rhizomes and roots (Table 3). In addition, stem density was positively correlated to the degree of stone embeddeness and the number of intersecting rhizomes. Correlations between F_C and both stone embeddedness and size were comparable

Table 2 Partial correlation coefficients between dependent variables (MANOVA)

	Depth	Flow†	Embeddedness	Wedge	α-axis†	Wetted	Thalweg	Epilithic plant cover	Stem density
F_C†	−0.26*	0.04	0.47***	0.18	0.35**	−0.12	0.04	0.01	0.13
Elimia abundance	−0.07	0.10	−0.18	−0.18	0.25*	−0.07	0.01	0.44***	−0.14
Epilithic plant cover	−0.04	0.23*	−0.38***	0.19	0.44***	0.32**	0.04	–	−0.19

†Log-transformed.
F_C: critical force needed to move stones; Wetted: relative distance to nearest wetted-edge of channel; Thalweg: relative distance to channel thalweg; Stem density: number of emergent *Justicia* stems within circular area (0.125 m²) around focal stones; d.f.: 72 for all correlations; *$P \leq 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 3 Partial correlation coefficients between dependent variables (MANOVA) for stones within *Justicia* beds where *Justicia* rhizomes and roots were measured (two Terrapin riffles and three Talladega riffles)

	Depth	Flow[†]	Embed	Wedge	α-axis[†]	Wetted	Thalweg	Stem density	Rhizomes	Roots
$F_C^†$	0.01	−0.04	0.56***	0.15	0.42***	−0.03	−0.14	0.10	0.42***	0.50***
Embed	−0.12	−0.26**	–	−0.07	0.13	−0.05	−0.14	0.23*	0.33***	0.33***
Rhizomes	−0.01	−0.14	0.33***	−0.12	−0.09	−0.17	−0.15	0.33***	–	0.24**

[†]Log-transformed.

F_C: critical force needed to move stones; Rhizomes: the number of *Justicia* rhizomes binding focal stones; Roots: presence or absence of attached roots to focal stones; d.f.: 119 for all correlations; *$P \leq 0.05$; **$P < 0.01$; ***$P < 0.001$.

with relationships found for the full (five streams) dataset (Tables 2 & 3).

Discussion

Substratum stability may be an important predictor of benthic invertebrate abundance and diversity within flood-prone streams (Cobb *et al.*, 1992; Death & Winterbourn, 1995). In addition, patches of stable substratum have been shown to be important refugia for benthic organisms during high flows (Francoeur, Biggs & Lowe, 1998; Suren & Duncan, 1999; Matthaei, Arbuckle & Townsend, 2000). The patch dynamics concept (*sensu* Townsend, 1989) predicts biotic diversity will be greater in more spatially heterogeneous environments because differential impacts of disturbance creates patches at varying stages of succession. Organisms within stable patches receiving minimal disturbance can therefore be important colonisation sources for more severely disturbed patches. Factors controlling the abundance and distribution of stable patches are, therefore, useful in understanding how communities recover or persist following disturbance.

In this study we showed that stones within *Justicia* beds were consistently more stable than stones elsewhere. Greater stone stability within *Justicia* beds was positively related to the degree of stone embeddedness and binding by rhizomes and roots. High streambed stability also has been shown to be influenced by embeddedness or bed packing in New Zealand and Australian streams (Downes *et al.*, 1998; Matthaei *et al.*, 1999). We found (within Talladega and Terrapin creeks) that embeddedness was positively related to the density of *Justicia* stems; this result supports our prediction that *Justicia* enhances the deposition of fine inorganic particles, presumably by decreasing flow. Moreover, rhizomes and roots

appeared to play a role in the greater F_C values for stones within *Justicia* beds.

Despite greater substratum stability within *Justicia* beds, epilithic plants and *Elimia* snails were not more abundant on stones associated with this macrophyte. However, our surveys were done during summer baseflow and on periods without floods (K.M. Fritz, personal observation). The annual peak discharge at downstream gauging stations occurred during the first week of April 2000, and at this time only Talladega Creek had a peak discharge with a 2-year return time (U.S. Geological Survey, unpublished data). Previous measures of the *Elimia* dispersal (Huryn & Denny, 1997; Johnson & Brown, 1997) indicate that 4–5 months is sufficient time for re-establishment of the preflood distribution. Therefore, the distribution of *Elimia* is unlikely to be governed by flood disturbance and the spatial patterns of substratum stability, but by other factors. For example, adult *Elimia* density was about three times higher in unshaded habitats with slow current in a Kentucky stream (Johnson & Brown, 1997). The abundance of epilithic algae (the primary food of *Elimia*) is probably higher outside *Justicia* beds because of greater shading within beds.

Determining if *Justicia* beds are refugia from bed-moving flows for benthic organisms, by sampling during summer baseflow rather than immediately following scouring spates, should have less consequence for epilithic plants than for snails because mosses and *Podostemon* are longer-lived and sessile. It was likely that most of the epilithic plants were exposed to spring floods prior to start of this study. However, the percent cover of epilithic plants was not higher within *Jusicia* beds. Perhaps the positive effect of enhanced substratum stability is counterbalanced by other physical factors in *Justicia* beds that reduce the establishment or growth of epilithic plants. On the

one hand, the emergent canopy of *Justicia* may reduce available light to submerged macrophytes and thereby restrict their distribution to areas with a low density of *Justicia* stems. On the other hand, many mosses grow well in low-light environments (Stream Bryophyte Group, 1999), so a reduction in light may not be the reason for low plant abundance, at least for mosses. Alternatively, it is possible that enhanced deposition of inorganic sediment within *Justicia* beds (i.e. high embeddedness) may either smother or reduce the colonisation of mosses (Suren, 1996); this latter mechanism, in addition to light limitation and reduced current velocity, may also inhibit colonisation by *Podostemum* (Munch, 1993; Connelly, Orth & Smith, 1999). Furthermore, there is some evidence for the inhibition of macrophyte seedling growth by leachates released from decomposing *Justicia* litter (Carter & Grace, 1986), which would be greatest in high-density *Justicia* patches.

Habitat modifiers are organisms that substantially alter their local environment and consequently may influence the distribution and abundance of neighbouring species (Bruno & Bertness, 2001). Unfortunately, little work has been done in stream communities to determine the degree to which habitat modifiers affect the distribution and abundance of neighbouring organisms. It is well-known that aquatic macrophytes alter surface and subsurface flow (e.g. Sand-Jensen, 1998; Dodds & Biggs, 2002), which in turn influence organic matter retention and other properties of the streambed associated with macrophyte beds (Sand-Jensen, 1998). Some bryophytes decrease the frictional drag and thereby enhance substratum stability (Suren *et al.*, 2000). Similarly, tussock grass leaf litter can stabilise substrata within artificial stream channels (Scarsbrook & Townsend, 1994). An exotic grass within a Sonoran Desert stream and *Carex* tussocks within a Californian stream increase the resistance of other aquatic and riparian plants to scouring floods (Dudley & Grimm, 1994; Levine, 1999). In addition to being efficient at trapping sediment, macrophyte beds may also be important flow refugia for benthic organisms, where animals can actively or passively colonise from areas with high shear stress (Lancaster & Hildrew, 1993; Winterbottom *et al.*, 1997). Based on our data it is tempting to suggest that *Justicia* may be an important habitat modifier in eastern North American streams and during scouring spates may function as stable

refugia. If *Justicia* contributes to the spatial variation in the physical structure of streams, it could be an important element in restoring degraded streams. However, our study was not designed to separate the presence of *Justicia* and spatial variation of substratum stability. We are conducting further experimental work to determine if the distribution of *Justicia* is a result of this patchiness in substratum stability or a cause of it.

Acknowledgments

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