



## Effects of disturbance type and microhabitat on species and functional diversity relationship in stream-bank plant communities

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### ABSTRACT

Spatial heterogeneity in site conditions and differing disturbance types are common features of natural landscapes. We asked: does the relationship between species diversity and functional trait diversity (SD-FD relationship) of plant communities vary among habitats experiencing different types of disturbance and among microhabitats (i.e., landscape position) within a landscape? We quantified the relationship between species richness and functional richness (FRic) and between species evenness and functional evenness (FEve) of riparian plant communities along small headwater streams at five spatially adjacent microhabitats in two types of disturbed (wildfire and clearcut logging with buffer) and reference habitats (unlogged mature forest) in north-western Ontario, Canada. We found significant dependence of species richness vs. FRic relationship on microhabitat, but not on disturbance type. Species evenness vs. FEve relationship varied slightly among reference and wildfire sites, but not among microhabitats. A significant variation in functional trait dispersion (FDis) among microhabitats offered a mechanistic explanation to the observed variation in the SD-FD relationship. A very weak effect of disturbance type on the SD-FD relationship indicates that clearcut with buffer retention may emulate riparian plant composition created by wildfire. However, the microhabitat dependent variation in the SD-FD relationship indicates that the same range of species diversity may refer to different ranges of functional trait diversity depending on microhabitat. We suggest that microhabitat plays a stronger role than disturbance type in trait dispersion and ultimately modifies the SD-FD relationship in our studied communities. This result highlights the role of spatial environmental heterogeneity of a landscape and different dimensions of species diversity and functional trait diversity, e.g. richness and evenness, in understanding the functioning of a natural landscape.

### 1. Introduction

Although species diversity has been a primary focus in assessing and managing ecosystems (Rodrigues et al., 2004), recently there has been increasing recognition of the value of using species traits to achieve that goal more effectively by assessing ecosystem functions and services (Díaz et al., 2007; Cadotte et al., 2011). Because diversity of functional traits (= functional trait diversity) is closely related to ecosystem functioning and services (Lavorel and Garnier, 2002), trait-based functional diversity is now preferred over taxonomy-based species diversity measures (Cadotte et al., 2011). While it is commonly assumed that species diversity is also linked to ecosystem functions and services or to functional diversity (Chapin et al., 1997; Tilman et al., 1997), few

studies have tested this assumption in heterogeneous natural systems (Duffy, 2009). Here we examine the relationship between species diversity and functional trait diversity (SD-FD relationship) in heterogeneous landscapes across microhabitats along the lateral gradients (riparian to upland forest) of small boreal streams that experienced different types of disturbance.

Earlier studies suggest that the SD-FD relationship is generally positive (Petchev and Gaston, 2002) but the relationship could vary with different factors. For instance, the sign of the SD-FD relationship could be negative, the slope of the relationship may vary from steep to flat and the shape parameter may vary from linear to non-linear/curvilinear with varying intensity of disturbance or site productivity (Mayfield et al., 2005; Flynn et al., 2009; Sasaki et al., 2009; Mayfield et al., 2010;

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Biswas and Mallik, 2011; Pakeman, 2011; Carmona et al., 2012; Luck et al., 2013). These variations in the SD-FD relationship are in-part governed by trait dispersion: strong trait filtering producing limited trait dispersion in a post-disturbance community may create different SD-FD relationship for pre- and post-disturbance communities, whereas weak trait filtering producing high trait dispersion may left the relationship unchanged (Mayfield et al., 2010; Biswas and Mallik, 2011). However, since disturbance is a key determinant of trait dispersion (Didham et al., 2005; Grime, 2006), different characteristics of a disturbance regime such as intensity, frequency, origin/type etc., are relevant to the SD-FD relationship. While earlier studies focused on disturbance intensity or site productivity, the role of disturbance type to the SD-FD relationship remains somewhat overlooked (Flynn et al., 2009; Massicotte et al., 2014). As the SD-FD relationship relates to functional redundancy (Biswas and Mallik, 2011; Luck et al., 2013), comparing the relationship among habitats experiencing different types of disturbance may offer useful insights into the resiliency of ecological communities (Mayfield et al., 2010).

In natural landscapes, disturbance may originate from anthropogenic land management and natural sources. These disturbances filter out non-compatible suites of traits, so that only a subset of species (from a reference habitat) with disturbance tolerance traits can occupy a disturbed habitat (Lavorel et al., 2007; Biswas and Mallik, 2011). While plant communities of boreal forests have evolved to be tolerant of periodic natural wildfires (Rowe, 1983; Allen, 2008), these communities may be less tolerant to relatively recent (in evolutionary terms) anthropogenic disturbance such as industrial forestry or urbanization (Lertzman and Fall, 1998). Accordingly, natural disturbances could promote functional group diversification or high trait dispersion (Drever et al., 2006; Clavel et al., 2011), whereas anthropogenic disturbances could lead to functional homogenization or limited trait dispersion (Abadie et al., 2011). Yet exceptions do exist. Reich et al. (2001) found similar species diversity or species composition in forest stands originated after logging compared to that after wildfire in the southern boreal forest of Minnesota. Hart and Chen (2008) found no difference in species richness and vegetation cover but species composition in post-logged and post-fire sites in the boreal forest of Ontario. In disturbance-adapted boreal forest of northwestern Ontario, the SD-FD relationship may thus vary between a disturbed habitat (treatment) and a control (reference) habitat, while the treatment-reference difference for the SD-FD relationship may be similar for both clearcut with buffer and natural disturbance treatments, e.g., wildfire.

However, natural landscapes are spatially and temporally heterogeneous (Wiens, 1989) where presence of different microhabitats and their spatial arrangement are important factors shaping species and trait distribution (Turner, 1989; Dupré and Ehrlén, 2002; Massicotte et al., 2014). Disturbance also interacts with landscape heterogeneity (Turner, 1989), so that disturbance effects on ecological structures or on the SD-FD relationship may not be uniform throughout the landscape (Fraterrigo and Rusak, 2008). Earlier studies examining the dependence of the SD-FD relationship on microhabitat focused on only highly contrasting microhabitats (Biswas and Mallik, 2011; Carmona et al., 2012). Yet in many natural landscapes, changes in contrasts of adjacent microhabitats in terms of difference in biotic and abiotic characteristics may be gradual, or at least may not be limited to two highly contrasting microhabitats (Biswas and Wagner, 2012). Understanding how the SD-FD relationship varies among adjacent microhabitats in the gradient dominated landscape remains unclear but necessary for managing this landscape.

In a gradient dominated landscape, plant communities at edges of habitats (ends of the gradient) are generally strongly influenced by the edge processes or by the extreme conditions of an underlying environmental gradient (Harper et al., 2005). In a riparian landscape, for example, stream influence (i.e., moisture gradient) on plant community is strongest at the stream banks, while the edge effects related to canopy openings created by clearcuts are strongest at the edge of a riparian

buffer (Braithwaite and Mallik, 2012; MacDonald et al., 2014). Note that, similar edge effects associated with canopy opening could be negligible at stream banks around small headwater streams, because canopies above small headwater streams are mostly closed. In this landscape, the SD-FD relationship is expected to vary among microhabitats, while disturbance effect on the relationship may be weaker in transitional microhabitats (e.g. stream bank or upland) than other microhabitats. This is because plant communities may exhibit greater trait divergence (high trait dispersion) in transitional microhabitat than either riparian or upland microhabitats (Biswas and Mallik, 2011).

A riparian landscape in the boreal forest is suited for this study, because of (i) periodic natural fire, flooding and clearcutting are integral factors known to shape the structure, composition and dynamics of riparian plant communities (Naiman et al., 2005; MacDonald et al., 2014), (ii) The riparian buffer and the land-water interface provide a conspicuous lateral environmental gradient (moisture, organic matter depth) extending from the water edge to the uplands. This creates diverse microhabitats, e.g. riparian → ecotone → mid-slope → edge → upland, presenting a gradient of biotic and abiotic heterogeneity at a very short distance (Braithwaite and Mallik, 2012).

Here we focus on two components of diversity, richness and evenness of species and functional traits (FRic- the amount of trait variability and FEve- the evenness of abundance distribution across species traits; cf. (Villéger et al., 2008)). The aim of our study is to test two predictions regarding the SD-FD relationship. (1) The relationship between species richness and FRic and between species evenness and FEve of plant communities in a reference habitat (unlogged mature forest) differ from that in a forest disturbed by periodic wildfire and clearcut with riparian buffer. (2) Disturbance effect on the relationship varies with microhabitats along a stream bank upland gradient. We do not hold separate predictions for richness and evenness components of the SD-FD relationship because of our primary interest on the relationship, which we define by pairing related components of species to functional trait diversity. We predict that reduced functional trait dispersion (FD) the degrees of divergence in abundance distribution of traits; cf. (Laliberté and Legendre, 2010)) in the disturbed sites compared to reference sites will offer a mechanistic explanation to the variation of the relationship.

## 2. Methods

### 2.1. Study system

We studied plant communities along lateral gradients of small headwater streams (catchment area: ~1 km<sup>2</sup>; average width: 1.04 m with a range of 0.43–1.77 m; shoreline slope: ≤15%) in the boreal forest of northwestern Ontario, Canada (Fig. 1). The study area is characterized by rolling topography with bedrocks overlain by glacial tills. Here, all streams visible in a 1:50 000 scale map are protected by riparian buffers (Ontario Ministry of Natural Resource, 1988). Common riparian plant species in the area are *Alnus incana*, *Cornus stolonifera*, *Calamagrostis canadensis*, *Thalictrum dayscarpum*, *Mertensia paniculata* and *Athyrium filix-femina*, and common understory species are *Ledum groenlandicum*, *Acer spicatum*, *Aster macrophyllus*, *Aralia nudicalus*, *Lycopodium annotinum* and *L. dendroideum*. The overstory vegetation is dominated by *Picea mariana* with dispersed *Picea glauca*, *Pinus banksiana*, *Abies balsamea*, *Populus tremuloides* and *Betula papyrifera*. Our selected stream sites were mostly dominated by *Picea mariana*. Additional site description and species composition can be found in Braithwaite and Mallik (2012).

### 2.2. Disturbance type and microhabitat

We considered two types of disturbed habitat (clearcut with buffer and wildfire burn sites) and a reference habitat (unlogged mature forest). Reference sites were approximately 60 to 90-yr old and

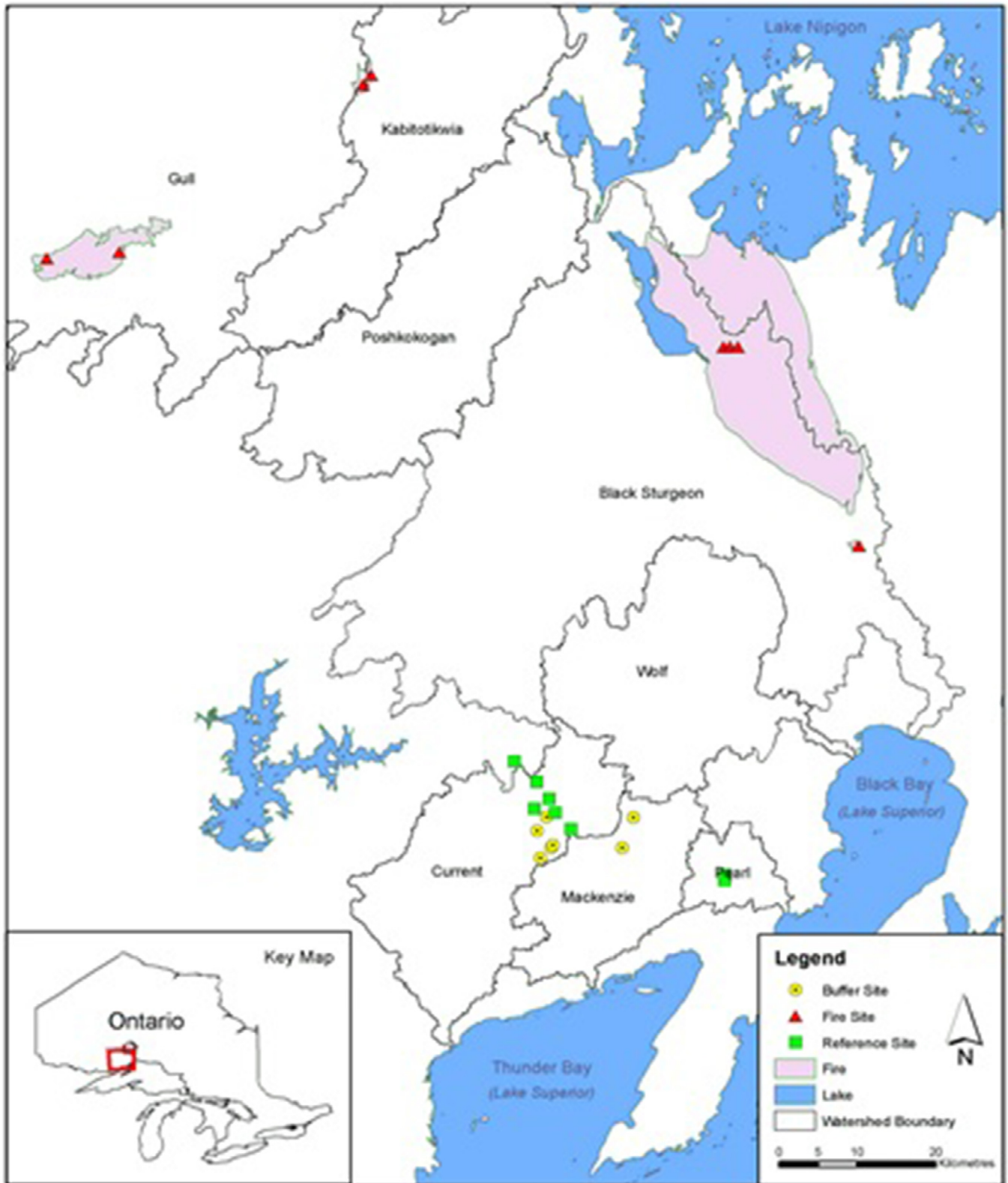


Fig. 1. A map of the study area showing study sites located in three watersheds near Thunder Bay; clearcut with buffer (circle), wildfire burned (triangle), reference (square).

wildfire-origin that had no land use activity within 500 m. According to Bridge (2001), fire return interval in northwestern Ontario is approximately 108 years; whereas, Ward et al. (2001) estimated that the fire return interval for northern Ontario forests could range from 190 years without fire suppression to about 600 years with fire suppression.

Clearcut sites were 2 to 6-yr old where riparian buffers were 28 to 52 m wide, extended on either side of a stream. Ages of uncut mature trees in the riparian buffers were approximately similar to that of trees in reference sites. Burned sites were 2 to 7-yr old, recovering from stand replacing wildfires. Selected burned sites were approximately

**Table 1**  
List of traits included in this study.

Trait	Scale	Description/categories
Raunkiaer life form	Nominal	mg: mega- or meso-phanerophyte ( $\geq 8$ m in height); mc: micro- or nano-phanerophyte (25–8 m); ch: chamaephyte (herb or shrub, but between 1 mm and 25 cm aboveground); h: hemicryptophyte (herb with bud at ground surface); g: geophyte (herb with underground bud); t: therophyte (annual)
Life cycle	Ordinal	1: annual; 2: biennial; 3: perennial
Flowering phenology	Nominal	sp: spring; su: summer; sf: summer-autumn
Stem tissue	Nominal	w: woody; n: non-woody.
Leaf persistence	Binary	0: no; 1: yes.
Principle means of reproduction	Nominal	1: seeds only; 2: vegetative propagation possible but mostly seeds; 3: mostly vegetation propagation
Seed dispersal vector†	Nominal	Mechanism of seed dispersal; wind, water, vertebrate, invertebrate
Seed banking	Ordinal	1: temporary; 2: persistent.
Fire resistance	Binary	0: no; 1: yes.
Flower colour	Nominal	w: white; g: unattractive (green or brown); b: bright (red, pink, yellow, blue or purple)
Growth rate	Ordinal	Growth rate after successful establishment relative to other species within same growth habit; slow, medium, rapid
Re-sprouting	Binary	Re-sprouting of woody species following top removal; 0: no; 1:yes
Anaerobic tolerance	Ordinal	Relative tolerance to anaerobic soil conditions; none, low, medium, high
Drought tolerance	Ordinal	Relative tolerance to drought conditions compared to other species with same growth habit; none, low, medium, high
Fire tolerance	Ordinal	Relative ability to re-sprout, grow, or reestablish from residual seed after fire; none, low, medium, high
Moisture use	Ordinal	Ability to use (i.e. remove) available soil moisture relative to other species; low, medium, high
Shade tolerance	Ordinal	Relative tolerance; intolerant, intermediate, tolerant.
Seed abundance		Amount of seeds produced by a particular plant species compared to other species with same growth habit; none, low, medium, high
Seed vigour	Ordinal	Expected seedling survival percentage of the plant species compare to other species with the same growth habit: low, medium, high
Seed spread rate	Ordinal	Capability of the plant species to spread through seed production compared to other species with the same growth habit: none, slow, moderate, rapid
Vegetative spread rate	Ordinal	Rate at which the plant species can spread compared to other species with same growth habit: none, slow, moderate, rapid

similar in the intensity of fires they experienced. While there was a difference in ages of reference and disturbed sites, ages of uncut mature trees in the riparian buffers were approximately similar to that of trees in reference sites. The selected sites were similar in tree species and stem density (Appendix A).

For microhabitats, we considered five spatially adjacent microhabitats along the stream lateral gradients, riparian, ecotone, mid-slope position, edge and upland, in each of the two disturbed and reference sites. These microhabitats were quite distinct with respect to habitat characteristics and plant species and trait composition (Braithwaite and Mallik, 2012; MacDonald et al., 2014). We defined (i) a riparian microhabitat as the point starting from the stream bank to the point where characteristic riparian vegetation was present, (ii) an ecotone as the point at which mature canopy trees were present or where we could visually recognize a shift in vegetation from riparian obligate species to those of typical upland species, (iii) a mid-position, representing the riparian buffer, as the approximate middle point of an ecotone and a buffer/fire edge position, (iv) a buffer edge as the position of canopy dip line of mature uncut trees, (v) a fire edge as the point at which there was minimal scorching to tall shrubs or location of live canopy trees, and (vi) an upland position as the position approximately 4 m away from edge position (in opposite direction).

### 2.3. Field sampling

Each of the two disturbance treatments and the reference conditions were replicated at eight stream sites, for a total of 24 small streams in this study. In each stream ( $N = 24$ ), we placed two perpendicular transects, separated by at least 50 m. Each transect was 64 m long at either side of a stream, starting at stream edge and running through five adjacent microhabitats on both sides of a stream. In each transect, we placed continuous 1 m<sup>2</sup> quadrats at 4 m intervals to reduce within microhabitat environmental heterogeneity and to minimize logistics (Braithwaite and Mallik, 2012). If 4 m interval did not match the ecotonal and the fire or buffer edge locations, additional contiguous quadrats were placed across the identified edges. The number of quadrats in each microhabitat was not uniform but on average had 2–3 quadrats, for a total of 827 quadrats in the study.

In each quadrat, we recorded presence of all vascular plants and visually estimated their percent cover (scale: > 0–100). Since site environmental conditions also moderate the SD-FD relationship (Pakeman, 2011), we considered soil moisture and canopy openness as potential covariates for this study. We measured soil moisture (by using a Delta H2 probe) and canopy openness (by using a crown densiometer) at the quadrat level. For soil moisture, three measurements were taken at three random locations within a quadrat and averaged them to represent the quadrat. All soil moisture measurements were taken within a period of seven days without any rainfall event.

### 2.4. Quantifying species and functional trait diversity

We recorded a total of 150 plant species. Based on the quadrat-level species presence and percent cover data, we calculated species richness and species evenness. Species evenness was quantified according to Pielou (1966) as,  $H'_{SD}/\log(S)$ , where  $H'_{SD}$  is Shannon's species diversity, which was defined as  $-\sum p_i \ln(p_i)$ , where  $p_i$  is the relative abundance of species  $i$  (MacArthur and MacArthur, 1961);  $S$  is the total species richness. There are several indices to quantify functional diversity (Mouchet et al., 2010). Since we focused on two key components of diversity i.e. richness and evenness, we quantified FRic and FEve as described by Villéger et al. (2008). FRic quantifies the amount of trait variability in a community and FEve describes the evenness of abundance distribution across species traits. For functional dispersion we quantified FDis, which describes the degrees of divergence in abundance distribution of traits in a community (Laliberté and Legendre, 2010). Nevertheless, across all sites, the higher the number of taxa sampled, the higher the diversity of traits represented (Appendix B). In the disturbed sites (clearcut and fire), however, the overall increase in functional diversity per unit of increase in the number of taxa occurred at a lower rate, perhaps due to the presence of functionally similar species in the disturbed habitat (Biswas and Mallik, 2011).

Functional diversity indices (FRic, FEve and FDis) were calculated by using function “dbFD”, which implements a flexible distance-based framework to compute multidimensional functional diversity indices, in the R library “FD”; we used Gower's distance and checked for correlation among traits. We used quadrat-level species percent cover matrix



**Table 2**

Results of mixed-effect models showing the effects of disturbance type and microhabitat on species richness and FRic relationships. Summarized ANOVA table was constructed by using function “anova” in the R library “car”. See appendix D for detailed coefficients.

<i>(a) Species richness-FRic relationship: reference vs. clearcut with buffer</i>					<i>(b) Species richness-FRic relationship: reference vs. wildfire</i>				
Model relevant to hypotheses					Fitted model				
	numDF	denDF	F-value	p-value		numDF	denDF	F-value	p-value
<i>Fixed effects</i>					<i>Fixed effects</i>				
(Intercept)	1	74	5330.27	< 0.0001	(Intercept)	1	75	5250.366	< 0.0001
Richness	1	74	223.92	< 0.0001	Richness	1	75	223.269	< 0.0001
Disturbance	1	14	1.243	0.2837	Microhabitat	4	60	0.875	0.4844
Microhabitat:Microhabitat	4	60	0.923	0.4565	Richness: Microhabitat	4	75	3.536	0.0107
Richness:Disturbance	1	74	0.868	0.3545	<i>Random effects (StdDev)</i>				
Richness: Microhabitat	4	74	3.502	0.0113	Site: 0.01915022 (intercept)				
<i>Random effects (StdDev)</i>					Site: 0.01949744 (intercept)				
Site: 0.01915022 (intercept)					Microhabitat %in% Site: 1.801055e−06 (intercept); 0.07073833(res)				
Microhabitat %in% Site: 1.801055e−06 (intercept); 0.07073833(res)					Site: 0.01949744 (intercept)				
AIC: −270.2585; BIC: −225.3003; LogLik: 150.1292					Microhabitat %in% Site: 1.964897e−06 (intercept); 0.07072254 (res)				
Residual autocorrelation: +0.384 (P < 0.0001)					AIC: −287.7804; BIC: −248.6421; LogLik: 156.8902				
					Residual autocorrelation: +0.370 (P < 0.0001)				

and a species-trait matrix with 21 categorical traits related to productivity, competitive ability, life history, stem tissue, phenology, flower colour, reproduction and adaption (Table 1). Choice of traits has important implications for studying the effects of disturbance or varying environmental conditions on the SD-FD relationship, because different traits may show different degree of convergence or divergence depending on site environmental conditions or disturbance (deBello et al., 2013; Carboni et al., 2014). Our chosen set of traits includes a mixture of competitive, disturbance tolerant and generalist traits (Biswas and Mallik, 2011), and thus this set of traits is less likely to produce biased response on the multi-trait indices due to disturbance or environmental conditions. Availability of trait data somewhat constrained our trait choice. We compiled trait data were from published literature (Biswas and Mallik, 2010) and the regional USDA plant data base (<http://plants.usda.gov/>).

2.5. Statistical analyses

To examine whether the relationships between species richness and FRic and between species evenness and FEve vary with disturbance type and microhabitat, we used linear mixed-effect modelling fit with Restricted Maximum Likelihood (REML) estimation (Zuur et al., 2009). We considered disturbance type and microhabitat as fixed factors and site as a random factor in which microhabitat were nested. We used microhabitat-wise average data (average of 2–3 consecutive quadrats at each microhabitat for both stream sides in each transect) for these analyses. Initially we included all relevant factors, interaction terms and covariates (soil moisture and canopy openness) in the statistical model. However, initial analysis revealed that covariate effects were statistically non-significant (Appendix C), and these environmental covariates were snap shot measurements. Therefore, we disregarded them from successive models. Final models were selected based on the

significance of a predictor term ( $\alpha = 0.05$ ) and the lowest AIC values (Burnham and Anderson, 2002; Zuur et al., 2009). However, since our hypotheses concerned about slope variations for disturbance type and microhabitat we kept disturbance type x species richness (or species evenness) and microhabitat x species richness (or species evenness) terms in our models, at least before fitting the final model (Eqs. (1–2)).

$$FRic \sim \mu + \beta_1 D + \beta_2 L + \beta_3 SpR + \beta_4 D^*SpR + \beta_5 L^*SpR + random$$

$$= 1|Site/L + \epsilon \tag{1}$$

$$FEve \sim \mu + \beta_1 D + \beta_2 L + \beta_3 SpE + \beta_4 D^*SpE + \beta_5 L^*SpE + random$$

$$= 1|Site/L + \epsilon \tag{2}$$

where  $\beta_{1-5}$  represent the regression coefficients associated with respective variables (D = disturbance type, L = microhabitat, SpR = species richness, SpE = species evenness).

We compared the relationship in the reference habitat with that in clearcut with buffer and in the reference with the wildfire in two separate analyses, instead of putting all the three disturbance types in the same model, because edge locations in the buffer and wildfire treatments differed markedly. Fire edges were adjacent to riparian areas (~9.2 m from stream bank), whereas buffer edges were bordering upland forests (~40.2 m from stream bank). Thus, their comparison may be ecologically less meaningful (Braithwaite and Mallik, 2012). The final fitted models for species richness–FRic relationship were identical for both reference vs. clearcut with buffer and reference vs. wildfire (Eq. (3)). For species evenness–FEve relationship, the final models for reference vs. clearcut with buffer (Eq. (4)) and reference vs. wildfire (Eq. (5)) were different.

$$FRic \sim \mu + \beta_2 L + \beta_3 SpR + \beta_5 L^*SpR + random = 1|Site/L + \epsilon \tag{3}$$

$$FEve \sim \mu + \beta_3 SpE + random = 1|Site/L + \epsilon \tag{4}$$

**Table 3**

Results of mixed-effect models showing the effects of disturbance type and landscape position on species evenness and FEve relationships. Summarized ANOVA table was constructed by using function “anova” in the R library “car”. See appendix D for detailed coefficients.

<i>(a) Species evenness-FEve relationship: reference vs. clearcut with buffer</i>					<i>(b) Species evenness-FEve relationship: reference vs. wildfire</i>				
Model relevant to hypotheses					Fitted model				
	numDF	denDF	F-value	p-value		numDF	denDF	F-value	p-value
<i>Fixed effects</i>					<i>Fixed effects</i>				
(Intercept)	1	74	49678.43	< 0.0001	(Intercept)	1	79	55766.15	< 0.0001
Evenness	1	74	68.21	< 0.0001	Evenness	1	79	69.12	< 0.0001
Disturbance	1	14	0.54	0.4755					
Microhabitat	4	60	0.77	0.5468					
Evenness:Disturbance	1	74	1.93	0.1687					
Evenness:Microhabitat	4	74	0.22	0.9239					
<i>Random effects (StdDev)</i>					<i>Random effects (StdDev)</i>				
Site: 0.009177188 (intercept)					Site: 0.007821192 (intercept)				
Microhabitat %in% Site: 0.008359798 (intercept); 0.03065352 (res)					Microhabitat %in% Site: 0.009937109 (intercept); 0.030044 (res)				
AIC: -562.3288; BIC: -517.3706; LogLik: 296.1644					AIC: -623.5521; BIC: -608.2391; LogLik: 316.776				
Residual autocorrelation: +0.143 ( <i>P</i> = 0.038)					Residual autocorrelation: +0.137 ( <i>P</i> = 0.045)				
<i>(a) Species evenness-FEve relationship: reference vs. wildfire</i>					<i>(b) Species evenness-FEve relationship: reference vs. wildfire</i>				
	numDF	denDF	F-value	p-value		numDF	denDF	F-value	p-value
<i>Fixed effects</i>					<i>Fixed effects</i>				
(Intercept)	1	74	68280.87	< 0.0001	(Intercept)	1	78	68099.94	< 0.0001
Evenness	1	74	103.62	< 0.0001	Evenness	1	78	103.72	< 0.0001
Disturbance	1	14	9.45	0.0082	Disturbance	1	14	9.42	0.0083
Microhabitat	4	60	0.96	0.4377	Evenness:Disturbance	1	78	4.21	0.0435
Evenness:Disturbance	1	74	4.55	0.0362					
Evenness:Microhabitat	4	74	0.91	0.4606					
<i>Random effects (StdDev)</i>					<i>Random effects (StdDev)</i>				
Site: 3.116922e - 06 (intercept)					Site: 1.503339e - 06 (intercept)				
Microhabitat %in% Site: 0.005758064 (intercept); 0.03580913 (res)					Microhabitat %in% Site: 0.00616932 (intercept); 0.03572207 (residual)				
AIC: -528.3677; BIC: -483.4095; LogLik: 279.1838					AIC: -573.5307; BIC: -552.1817; LogLik: 293.7654				
Residual autocorrelation: +0.119 ( <i>P</i> = 0.068)					Residual autocorrelation: +0.077 ( <i>P</i> = 0.161)				

$$FEve \sim \mu + \beta_1 D + \beta_2 SpE + \beta_3 D * SpE + random = 1 | Site/L + \epsilon \quad (5)$$

We checked spatial autocorrelation in the original response or predictor variables and in the residuals and found weak but significant (except evenness of reference vs. wildfire) spatial autocorrelations (residual autocorrelation values ranges from 0.19 to 0.38 for richness models and 0.07–0.14 for evenness models; see Tables 2, 3). Residual spatial autocorrelation can result in poor model fit or incorrect hypothesis testing, although the parameter estimates are generally little affected (Karpievitch et al., 2009). Such spatial structures can be modeled by including spatial correlation structure in the mixed-effects model (Zuur et al., 2009). Based on visual assessment of residuals, we included a spherical correlation structure in the statistical model but the log-likelihood ratio test revealed that models with and without correlation structures did not differ significantly. Also, there was no significant improvement in model AICs when spatial correlation structure was included. Thus, we fitted statistical models without spatial correlation structure (Eqs. (3–5)). Nonetheless, there was no major qualitative difference in the results of mixed effects models with and without correlation structure (results not shown).

To test whether mean FDis varied between different types of disturbance and between landscape positions we conducted a linear mixed effects model analysis where disturbance type and landscape positions were treated as fixed factors and site as a random factor in which landscape positions were nested in. All analyses were performed in the statistical programme R by using packages “nlme”, “car”, “lsmeans” and “spdep”.

### 3. Results

#### 3.1. Species and functional richness and evenness

Both species richness and FRic were slightly higher (but statistically

non-significant) in the clearcut with buffer treatment than the reference or the wildfire treatment, and significantly higher in riparian microhabitat than others (Fig. 2). After accounting for the random effects associated with sites and microhabitats nested within sites, there was no statistically significant difference in mean FRic between reference and clearcut with buffer or between reference and wildfire treatments, but differed among microhabitats (Table 2, Fig. 2). On the other hand, species evenness and FEve were somewhat similar for clearcut with buffer, the reference or the wildfire treatment (Fig. 2). After accounting for the random effects associated with sites and microhabitats nested within sites, there was no significant difference in mean FEve between reference and clearcut with buffer; however, reference and wildfire sites were significantly different (Table 3). FEve did not differ significantly among microhabitats (Table 3, Fig. 1).

Over the entire data set, there was a weak correlation between species richness and species evenness (Pearson’s correlation coefficient,  $r = 0.27$ ;  $P < 0.01$ ) and between FRic and FEve ( $r = 0.15$ ;  $P < 0.05$ ), implying that richness and evenness indices captured relatively unique information. There were strong to moderate correlation between species richness and FRic ( $r = 0.82$ ;  $P < 0.01$ ) and between species evenness and FEve ( $r = 0.62$ ;  $P < 0.01$ ), confirming the natural relationship among these indices.

#### 3.2. Effects of disturbance type on the SD-FD relationship

Contrary to our prediction, slope of the species richness-FRic relationship did not vary between the reference and the clearcut with buffer sites or between the reference and the wildfire sites (Table 2; Fig. 3). Slope of the species evenness-FEve relationship also did not vary between the reference and clearcut with buffer treatment comparison but varied significantly between the reference and the wildfire treatment (Table 3; Fig. 3). That is, the overall role of disturbance type

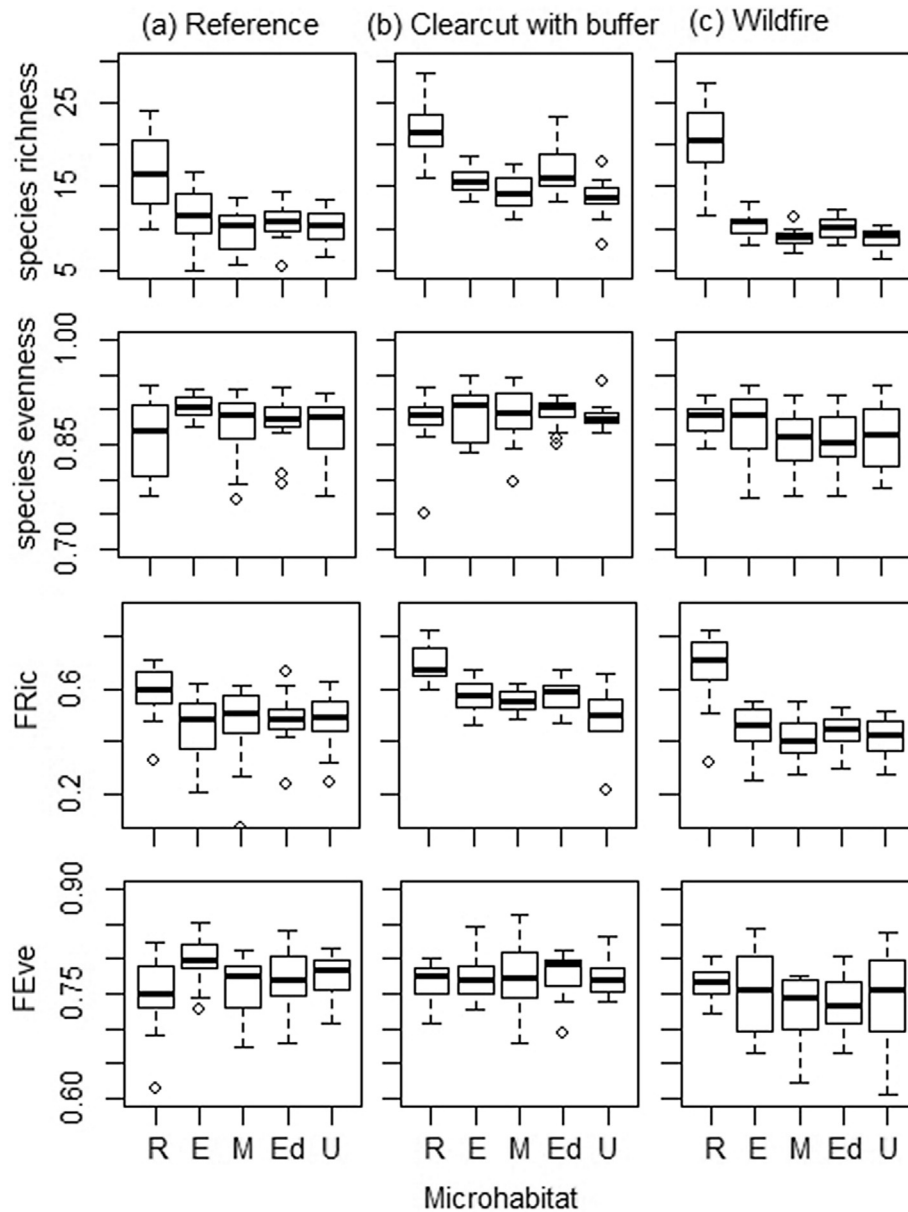


Fig. 2. Box plots showing species richness, species evenness, FRic and FEve of riparian plant communities in reference, clearcut with buffer and wildfire sites in different microhabitats along a stream bank –upland gradient (R = riparian, E = ecotone, M = mid-slope, Ed = edge, U = upland).

moderating the SD-FD relationship seemed very weak.

### 3.3. Effects of microhabitat on the SD-FD relationship

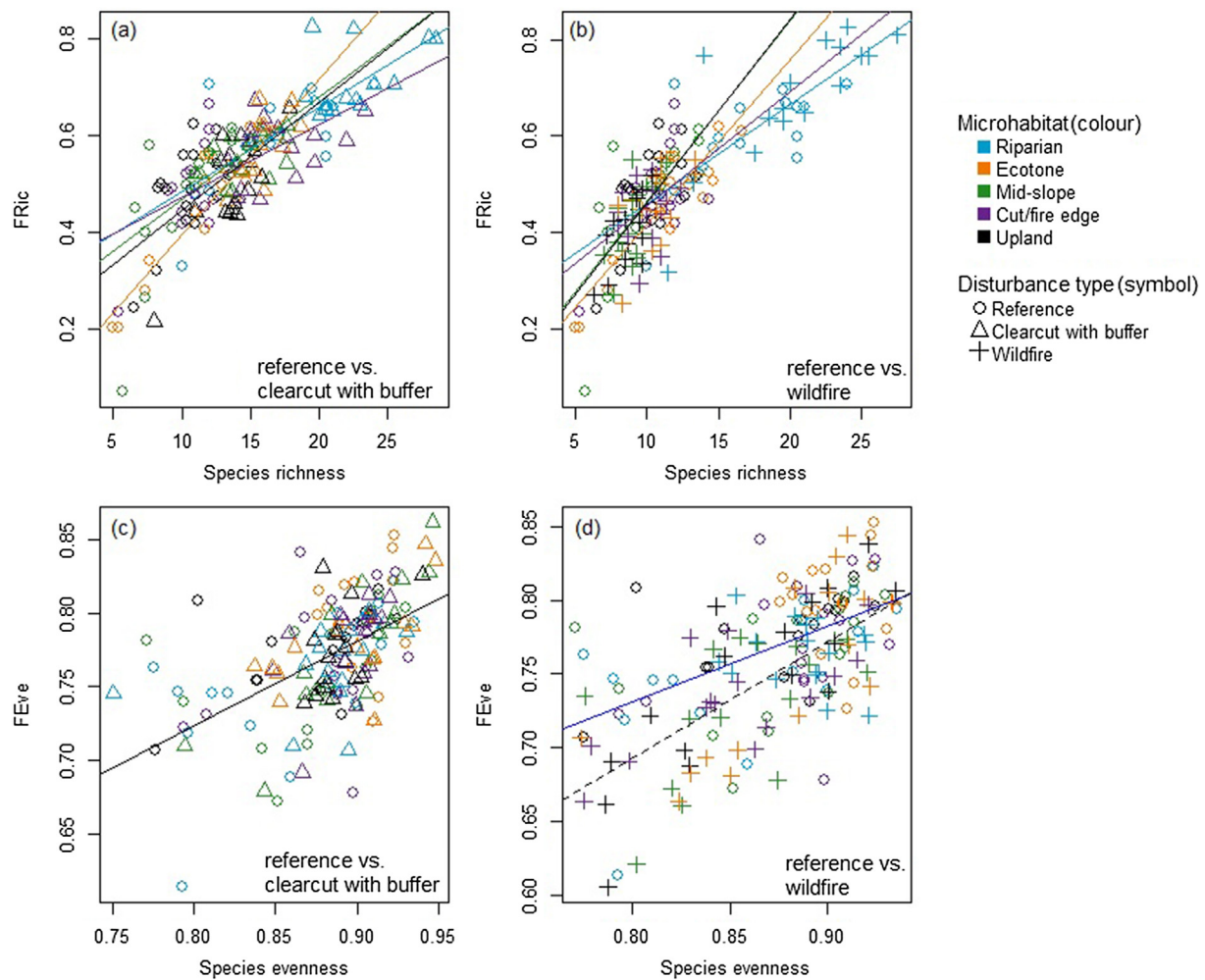
As predicted, the slope of the species richness-FRic relationship significantly varied between different microhabitats for both reference vs. clearcut with buffer and reference vs. wildfire models and (Fig. 3; Table 2). Interestingly, when we pooled data across wildfire and reference we found a consistent pattern of slope increase in richness relationship from stream bank to upland (slope coefficient reference vs. wildfire:  $0.020_{\text{riparian}} \rightarrow 0.020 + 0.014_{\text{ecotone}} \rightarrow 0.020 + 0.017_{\text{mid slope}} \rightarrow 0.020 + 0.003_{\text{fire edge}} \rightarrow 0.020 + 0.018_{\text{upland}}$ ; Appendix D). Such pattern held true for clearcut with buffer vs. reference model as well: slope increased from stream bank to upland, except for a slight reduction at the cut edge (slope coefficient reference vs. clearcut with buffer:  $0.017_{\text{riparian}} \rightarrow 0.017 + 0.015_{\text{ecotone}} \rightarrow 0.017 + 0.004_{\text{mid slope}} \rightarrow 0.017 - 0.002_{\text{cut edge}} \rightarrow 0.017 + 0.005_{\text{upland}}$ ). However, for species evenness-FEve relationship, slope did not vary with microhabitat, for both reference vs. clearcut with buffer and reference vs. wildfire models (Table 3).

### 3.4. Effects of disturbance type and landscape position on functional dispersion (FDIs)

As predicted, functional dispersion of traits (FDIs) significantly varied with microhabitats (Mixed effect model: microhabitat effects:  $F_{4,84} = 8.82$ ;  $P < 0.001$ ): FDIs decreased consistently from stream bank to upland (Fig. 4). However, the effects of disturbance type ( $F_{2,21} = 2.09$ ;  $P = 0.1483$ ) or the disturbance type-microhabitat interaction effect on FDIs was not significant ( $F_{4,84} = 1.44$ ;  $P = 0.1926$ ). That is, compared to disturbance type, microhabitat had a stronger control in trait dispersion of riparian plant communities.

## 4. Discussion

We found slightly higher (but statistically non-significant) mean species richness in the clearcut with buffer sites than in the reference or burned sites. We also failed to detect statistically significant difference in mean functional richness and functional evenness between reference and clearcut with buffer or between reference and wildfire treatments.



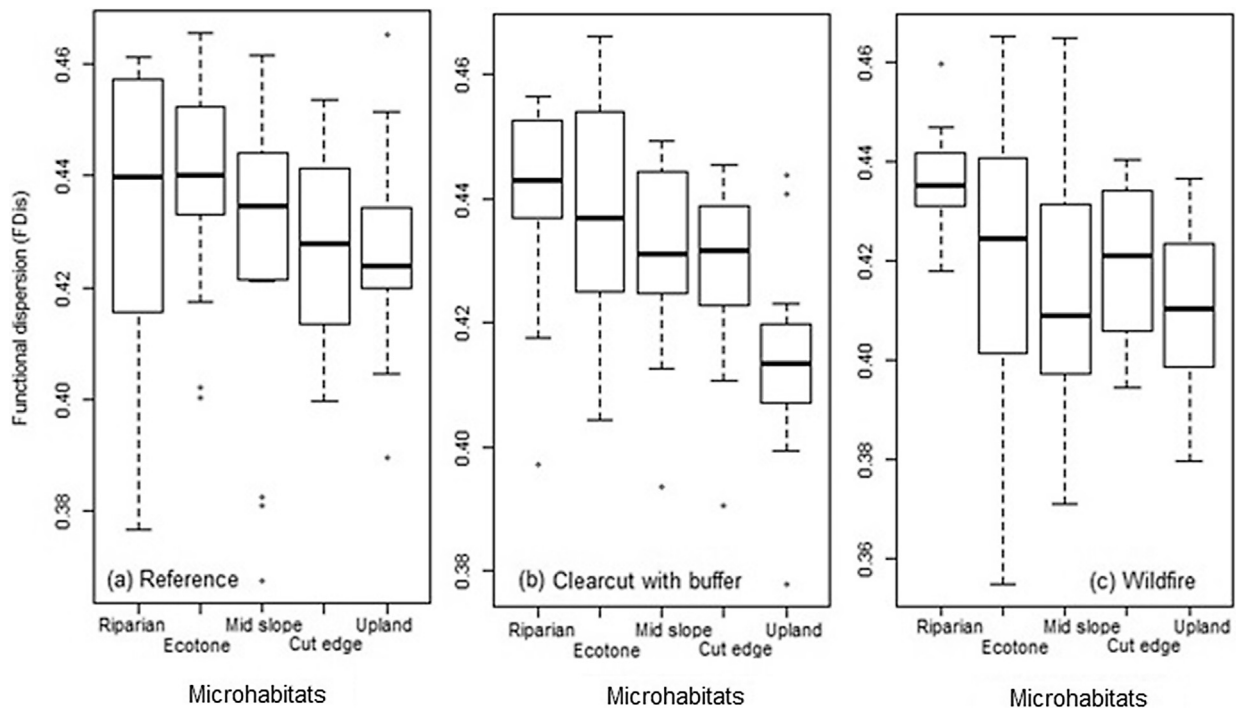
**Fig. 3.** Relationship between species richness and FRic (a, b) and species evenness and FEve (c, d) for reference vs. clearcut with buffer (a, c) and for reference vs. wildfire sites comparison (b, d). Empty circles represent reference sites (O), while triangles and cross represent clearcut with buffer ( $\Delta$ ) and wildfire (+) sites, respectively. Since mixed effects models showed dependence of the species richness-FRic relationship on microhabitat, we fitted different slopes and intercepts for each microhabitat (riparian = sky blue, ecotone = orange, mid-slope = green, cut/fire edge = purple, upland = black). Species evenness-FEve relationship did not vary among reference and clearcut with buffer sites, but varied among reference and wildfire sites, thus we fitted identical slope and intercept in the first comparison (c) and different slopes and intercepts for the later (d).

Consistent with Lamb et al. (2003), these results implicate that riparian plant communities around small streams in our studied communities are not affected by upland clearcut or fire disturbance. Most riparian plant species can colonize bare sediments and also possess the trait of aggressive clonal growth that allow rapid recovery following clearcut or fire (Naiman et al., 2005). Many of the riparian species are also long lived perennials (Lamb and Mallik, 2003), meaning that if individual plants are not directly damaged by the clearcut or fire, then they can persist. As long as a clearcut or fire in the uplands does not result in important and long-term changes in the stream hydrology and thus the regeneration and establishment conditions, then there should be no major changes in the riparian zone vegetation (Lamb et al., 2003). Alternatively, the non-significant result could be related to statistical power in our study. The post-hoc power analysis (Gałecki and Burzykowski, 2013) across microhabitats revealed that the statistical power to detect the species richness difference between reference versus clearcut with buffer (effect size, +4.75) and wildfire ( $-0.07$ ) site was 0.83; whereas, the statistical power to detect the functional richness and functional evenness difference between reference versus clearcut with buffer (effect sizes for functional richness and evenness, +0.08 and 0.002) and wildfire ( $-0.02$  and  $-0.03$ ) sites were 0.36 and 0.33, respectively. That is, although we had a modest statistical power to detect the species richness difference, we had low statistical power to

detect functional (richness and evenness) differences. Therefore, we suggest cautious interpretation of our results. We further suggest that higher sampling effort is needed to detect functional difference than taxonomic difference in plant communities experiencing different types of disturbances in this landscape.

We found strong dependence of the species richness vs. FRic relationship on microhabitat (Fig. 3). We suggest that the degrees of trait dispersion (measured by FDis) is a potential mechanism underlying the variation in the species richness vs. FRic relationship. As the species richness vs. FRic relationship was varying from stream bank to the upland, FDis was also decreasing consistently (Fig. 4), perhaps due to species dispersal limitation or to site productivity (Biswas and Mallik, 2010). Wildfire and clearcuts along small streams commonly lead to physical deformation of the stream bed and accumulate slash or burned materials in the stream that interrupt stream flow (Mallik et al., 2011). Water dispersed plant propagules may thus experience dispersal limitation, especially in the disturbed habitats (Biswas and Mallik, 2010). Stream banks are also productive microhabitats in terms of high soil moisture, organic matter and nutrients, which can support plants from diverse functional groups (high trait dispersion or high FDis), whereas upland microhabitats may filter out most species with disturbance tolerance traits, i.e., limited trait dispersion (Biswas and Mallik, 2011). While we did not focus on the response of individual traits here due to





**Fig. 4.** Box plots showing FDis of riparian plant communities in reference, clearcut with buffer and wildfire sites in different microhabitats along a stream bank–upland gradient. FDis did not vary among disturbance types but varied significantly among microhabitats. The post-hoc analysis revealed the following groupings: Riparian<sup>a</sup> → Ecotone<sup>ab</sup> → Mid-slope<sup>bcd</sup> → Cut/fire edge<sup>bcd</sup> → Upland<sup>d</sup> where microhabitat denoted by the same superscript did not differ significantly at  $\alpha = 0.05$ .

our primary focus on the multi-trait indices, such results are presented elsewhere (Biswas et al., 2016) and the results indicate that different traits may respond to disturbance differently (deBello et al., 2013; Carboni et al., 2014). Therefore, it would be interesting to study the SD-FD relationship with different suits of traits or explore the response of individual traits in future.

The slope of the species richness vs. FRic relationship signifies the marginal contribution of a species to the FRic or ecosystem functioning: the steeper the slope, the higher the contribution a species to ecosystem functioning. Such contribution of a species to SD-FD slope is likely to be stronger in a species and functionally rich vs. species and functionally poor habitat (Biswas and Mallik, 2011); conversely, the marginal effect of species loss on ecosystem function may be relatively less consequential in a functionally diverse habitat than habitats with species from few functional groups. The stream bank riparian microhabitats are relatively diverse (species and functional richness) compared to the uplands (Fig. 2) and the slope of the SD-FD relationship became steeper from stream bank to upland (Fig. 3), implying that plant communities along stream bank microhabitat are more resilient or they recover more quickly than the upland microhabitats.

However, although we expected a weaker degree of slope variation at the uplands due to high trait dispersion associated with edge effects, such effects on plant functional traits seemed weak and we found limited trait dispersion (Fig. 4) causing relatively strong slope variation (Fig. 3). Edge effect on plant community varies with time, environmental site conditions and forest types (Harper et al., 2005). While Braithwaite and Mallik (2012) found significant edge effects on environmental factors in this system, probably it was too early (2–6 yrs old) to find such effects on plant functional types.

We found that disturbance type had a weak effect on the species evenness and FEve relationship. In particular, species evenness and FEve relationship varied among the reference and wildfire sites but not among the reference and clearcut with buffer sites (Fig. 3). Earlier studies have shown that species and trait composition in wildfire sites correspond to undisturbed reference sites or to clearcut with buffer sites (Lamb and Mallik, 2003). However, given that species and trait

composition or the SD-FD relationship of plant communities may vary between clearcuts and its nearby buffer strips (Biswas and Mallik, 2011), retention of buffers may be a key factor producing similar responses in the SD-FD relationship across disturbance types (Macdonald et al., 2004). A riparian buffer may create positive effects on species dispersion and may thus quickly nullify the adverse effects of clearcut (Drever et al., 2006). As well, we did not find any evidence varying functional dispersion depending on disturbance type. While this results may indicate that clearcut with buffer retention may emulate riparian plant composition created by wildfire in our studied communities (Macdonald et al., 2004), we suggest for cautious interpretation of our result due to our focus on short-term response (2–7 yrs) (Kreutzweiser et al., 2012). On the other hand, Kreutzweiser et al. (2008) found that clear-cut logging negatively affect stream micro-invertebrate community; therefore, assessment of important aquatic ecosystem process is also important to comprehensively understand how clearcut disturbance may mimic the ecological conditions created by wildfire (Kreutzweiser et al., 2012).

Dependence of species richness relationship, but not species evenness relationship, on microhabitat implies that ecological factors or processes operate at different spatial scales (deBello et al., 2013). While both species richness-FRic and evenness-FEve relationships are likely to be affected by disturbance at a similar spatial scale, richness relationship seems more sensitive to processes operating at a finer spatial scale and the relationship varied among microhabitat. This result is puzzling given that species richness and FRic is generally sensitive to environmental filtering, whereas species evenness and FEve reflects fine-scale niche partitioning within the framework of environmental filtering and species interactions (Mouchet et al., 2010). However, a single ecological process can be reflected on multiple dimensions of species and functional trait diversity or multiple ecological processes can be reflected on a single dimension (Mouchet et al., 2010). Further complexity arises in empirical studies where processes themselves interact or processes relevant to composition and configuration of landscape interact with environmental filtering or niche partitioning (Münkemüller et al., 2012). Further experimental or simulation study is

required to understand the sensitivity of these indices to landscape-level processes.

## 5. Conclusions and management implications

We demonstrate that in post-harvest and post-fire riparian habitats species and functional trait diversity and the relationship between them vary with microhabitats within a landscape, and disturbance type has a very weak effect on the SD-FD relationship. This results imply that higher species diversity may not ensure equally higher level of trait representation across microhabitats in disturbed riparian landscape. That is, the linkage between species diversity and ecosystem functioning or functional trait diversity is inconsistent, especially in post-disturbed heterogeneous landscapes. Hence, we suggest that species diversity alone may not be a good proxy for ecosystem functioning in naturally heterogeneous landscapes. While it is too early to suggest any specific management prescription based on our study, land managers need to consider the different dimensions of species diversity and functional trait diversity e.g. richness and evenness to monitor the health of riparian ecosystems experiencing disturbance (Cadotte et al., 2011).

A very weak effect of disturbance type on SD-FD relationship indicates that clearcut harvesting with buffer retention may emulate plant community compositions created by wildfire (Sibley et al., 2012). However, the microhabitat dependent variation in the SD-FD relationship indicates that the same range of species diversity may refer to different ranges of functional trait diversity depending on microhabitat. We hypothesize that microhabitat plays a stronger role than disturbance type in trait dispersion, which ultimately modifies the SD-FD relationship in our studied communities (Biswas and Mallik, 2011). This result highlights the role of spatial environmental heterogeneity of a landscape affecting the functioning of a natural landscape following disturbance.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.10.021>.

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