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Pioneer annual vegetation of gravel-bed rivers: first insights on environmental drivers from three Apennine streams

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ABSTRACT

A huge knowledge gap exists on riverine pioneer vegetation. Despite its relevance in regulating the C metabolism at the catchment scale, and the triggering role in shrubs and trees establishment along riverbanks, little data is available on its environmental determinants. Indeed, most existing knowledge in this field refers to woody species or aquatic macrophytes neglecting the ecosystem relevance of ephemeral herbaceous vegetation. Focusing on three gravel bed rivers located in northern Italy (Baganza, Nure and Parma streams), the present study is aimed to evaluate the riverine ephemeral plant richness, considering both native and alien *taxa*, and the role of hydrogeomorphological disturbance and sediment quality in the observed richness patterns. At higher disturbance rates (*e.g.*, larger river sizes), our data indicates a progressive decrease in overall plant richness, but also an increase in the coverage-abundance rates mainly due to alien species. This evidence confirms that variations in hydrology imply changes in pioneer plant species richness at in-stream periodically exposed sediments. More attention must be given to the vulnerability of pioneer vegetation to climate change and direct human impacts to fully understand the functioning of lotic ecosystems, especially the non-perennial ones.

INTRODUCTION

In recent years, the quantification of the interactions between hydromorphological processes and vegetation has supported the development of multiple conceptual models able to predict the responses of riverine plants to water force (Corenblit *et al*., 2007; Gurnell *et al*., 2016). A major output of these research advances is the identification of "critical zones" for physical ecosystem engineering of fluvial systems mediated by plants (Gurnell *et al.*, 2016), where patchy vegetation assemblages interact directly with the fluvial disturbance and can partially drive the riverine evolution processes (Leyer, 2006; Corenblit *et al*., 2007).

About this, most of the available knowledge refers to woody species or aquatic macrophytes - identified as key "ecosystem engineers" (Thomaz and Cunha, 2010) - neglecting the ecological importance of ephemeral herbaceous vegetation and its ecological determinants (Leyer, 2006; Corenblit *et al.*, 2014). Indeed, only few contributions explored the biological features of pioneer plants, focusing on exposed muds and marginal lentic water bodies, or on the role of river-floodplain connectivity in driving their multi-spatial distribution patterns (Salisbury, 1970; Leyer, 2006; Bolpagni and Piotti, 2015, 2016). Even if this vegetation plays a minor role in modulating the river dynamics, from a morphodynamical point of view these plant communities represent the initial stages of the establishment of shrubs (*e.g.*, *Salix* spp.) and trees (*e.g.*, *Populus nigra* L., *Salix alba* L.). Therefore, pioneer vegetation is involved in key functions such as regulating the mobility of river edges and creating landforms (Gurnell *et al.*, 2012, 2016). Moreover, a growing number of data demonstrates the crucial role of riverine ephemeral vegetation in modulating the C metabolism at the catchment scale (Bolpagni *et al.*, 2017, 2019; Mallast *et al.*, 2020), with relevant implication on stream/river functioning (Gómez-Gener *et al.*, 2021).

Furthermore, pioneer vegetation is also expected to have a high sensitivity to climate change, especially in the temperate regions where substantial changes in river discharges and flood magnitude are probable in the next decades, as well as the recurrence of flow cessation events (Datry *et al.*, 2014; Messager *et al.*, 2021). Lastly, pioneer annual vegetation of river corridors - comprised in the *Chenopodion rubri* and *Bidention tripartitae* alliances - has been recognized as habitat of high conservation value by European designation [*e.g.*, Annex I habitat in the EC Habitats Directive (92/43/EEC)]. It attains higher values of plant diversity compared to contiguous shrubby and woody stands, although riverine herbaceous stands are

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characterized by a greater “biotic acceptance” of alien species as richness in native species increases (Corenblit *et al.,* 2014).

In this context, it becomes critical to integrate available knowledge on the role of hydrogeomorphic disturbance in driving herbaceous plant species richness to relate alien and native species along gradients of river discharge (Burkart, 2001; Corenblit *et al.,* 2014). We expected that the abiotic determinants (*e.g.*, flow and sediment granulometry) significantly explain the diversity patterns of ephemeral vegetation. Starting from this hypothesis, the present paper aimed at quantifying plant richness responses to the hydrogeomorphological disturbance (expressed in terms of river discharge and topography) and sediment quality (expressed in terms of granulometry), considering the contribution of both native and alien *taxa.*

METHODS

Study area

The study was carried out along three gravel bed rivers (Baganza, Nure and Parma streams) located in the Po Plain (northern Italy) (Fig. 1). The Po Plain is characterized by a mild continental climate with annual rainfall of ~1000-1200 mm year^{-1} concentrated during fall (October-November). These streams have a pluvial hydrological regime with a predominant natural regulation. Their mean annual discharges for the period 1991-2011 are 5.2, 8.6 and 13.3 m^3 s^{-1} for Baganza (BA), Nure (NU) and Parma (PR) streams, respectively; the bankfull width (mean±standard deviation) ranges from 117±35 m (BA) to 191±40 m (PR) (Burgazzi *et al.*, 2017, 2020).

In the highly dynamic piedmont zone of each river, a study site was chosen corresponding to a stretch of approximately 600 m length, enclosing an active stretch with similar characteristics (*e.g.*, meso-habitats arrangement). In presence of a braided behavior, data was collected along the main reach to consider riparian margins with equivalent hydrogeomorphic characteristics and to collect comparable results among streams.

Experimental design and vegetation characterization

During late summer 2014, at each study site herbaceous vegetation was described in 15 randomly distributed plots of 4 m^2, in agreement with Chytrý and Otypková (2003) and Corenblit *et al.* (2014). All the species (both native and alien) were recognized, and their ground-projected cover area was estimated by 5-per-cent-cover classes (from 0 to 100%) assigning 1% and 3% respectively to rare and sporadic species (with cover-abundance percentages lower than 5%). Plant nomenclature follows Bartolucci *et al.* (2018) for native species, Galasso *et al.* (2018) for the alien plants, and the updates reported by the Portal to Flora of Italy (http://dryades.units.it/floritaly/). Here, for alien *taxa* we considered both neophytes - including all *taxa* introduced after 1492 AC by humans - and archeophytes (Galasso *et al.,* 2018). A specification is necessary for *Setaria italica* (L.) P.Beauv. ssp. *viridis* (L.) Thell. and *Xanthium italicum* Moretti, two of the most spread species in the riparian herbaceous vegetation in the Po basin (Bolpagni and Piotti, 2015, 2016), that must be considered, despite their specific epithets, alien *taxa* (Banfi and Galasso, 2010). *Bidens vulgata* Greene and *Bidens frondosa* L. have been grouped due to the impossibility of differentiating them as immature individuals.

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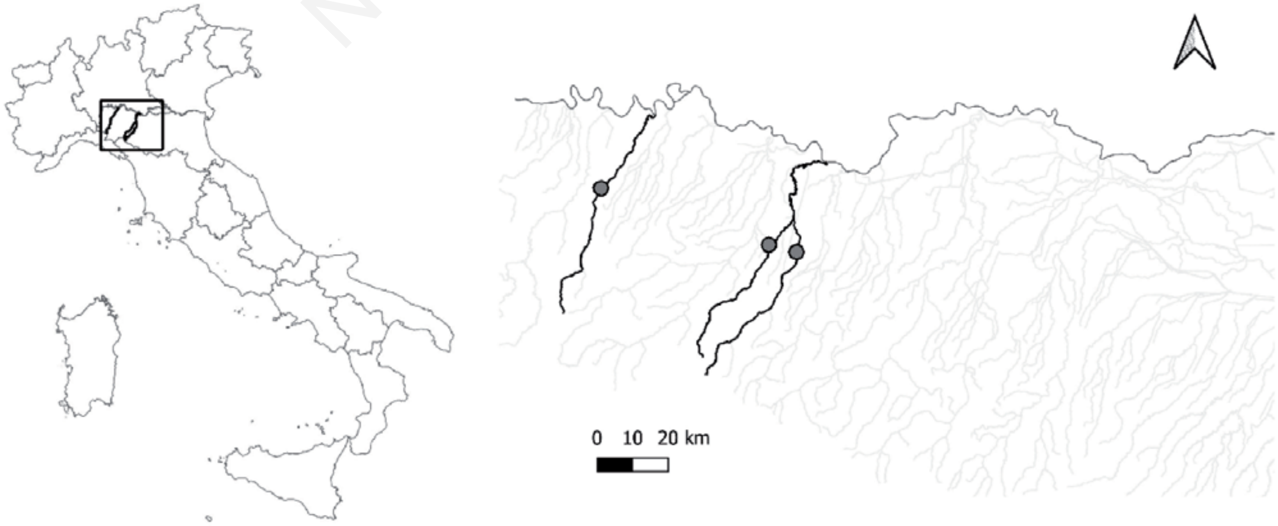

Fig. 1. Map of the study area with the location of sampled river stretches.

Environmental driver characterization

Simultaneously with the vegetation characterization, the main hydrogeomorphic features of each study plot were estimated (Corenblit *et al.,* 2014). The topography (HT = height above water base flow level) was characterized in relation to the summer base flow of the main channel during the study period by measuring the elevation and the distance (expressed in m) from the active river channel edge. Surface sediment texture (ST) was defined in agreement with Wolman (1954).

Data analysis

A one-way ANOVA was performed on environmental determinants (HT and ST) data to account for the relative effect of site in R environment (R Core Team, 2021). Linear mixed models were used to test the effect of HT and ST on species richness and abundance, setting the site as random effect and HT and ST as fixed effect. We tested the models separately using the following response variables: total species richness (TR), native species richness (NR), alien species richness (AR), ratio between alien and native species richness (AR/NR) and ratio between alien and native species cover (AC/NC). Important outliers were removed from the dataset, and data was checked for assumptions before running the analyses. Data was not transformed although in some cases normality of residuals was not entirely met, because we found negligible differences in the outputs between the transformed and non-transformed models. All models were run in R environment, using the package "lmerTest" (Kuznetsova *et al.*, 2017; R Core Team, 2021).

RESULTS

Environment drivers

The relative elevation of plots ranged between 10 and 146 cm above the summer base-flow level of studied streams. A significant increase in elevation as the mean river discharge increases was observed (one-way ANOVA, F = 5.140, p=0.010). HT peaked at PR plots (69±39 cm), whilst the lowest average values were recorded at BA (35±18 cm) (Fig. 2). No statistical differences between rivers in sediment texture properties were observed (one-way ANOVA, F = 0.7177, p=0.494) (Fig. 2). The average diameters of particle axes ranged between 2.2±0.6 cm (NU) and 2.4±0.6 cm (PR).

Species richness and cover

A total of 108 species was recorded, 68 *taxa* at PR sites (equal to 63% of the overall recognized species), and 66 *taxa* at BA and NU sites (61%). The most widespread species, recorded at least in 50% of the sampled plots (= 22) , were eight, with *Xanthium italicum*, *Persicaria lapathifolia* (L.) Delarbre ssp. *lapathifolia*, *Echinochloa crus-galli* (L.) P. Beauv., *Setaria italica* ssp. *viridis*, *Populus x canadensis* Moench, *Ambrosia artemisiifolia* L. and *Bidens vulgata/frondosa* found in 65% or more of sampled plots. *X. italicum*, an alien *taxon*, and *P. lapathifolia* ssp. *lapathifolia* were the only two species recorded in all the investigated plots (Tab. 1). The alien *taxa* accounted for 32.4% (35 *taxa*) of the total diversity - and overall, they can be considered invasive, as for example *A. artemisiifolia, Artemisia*

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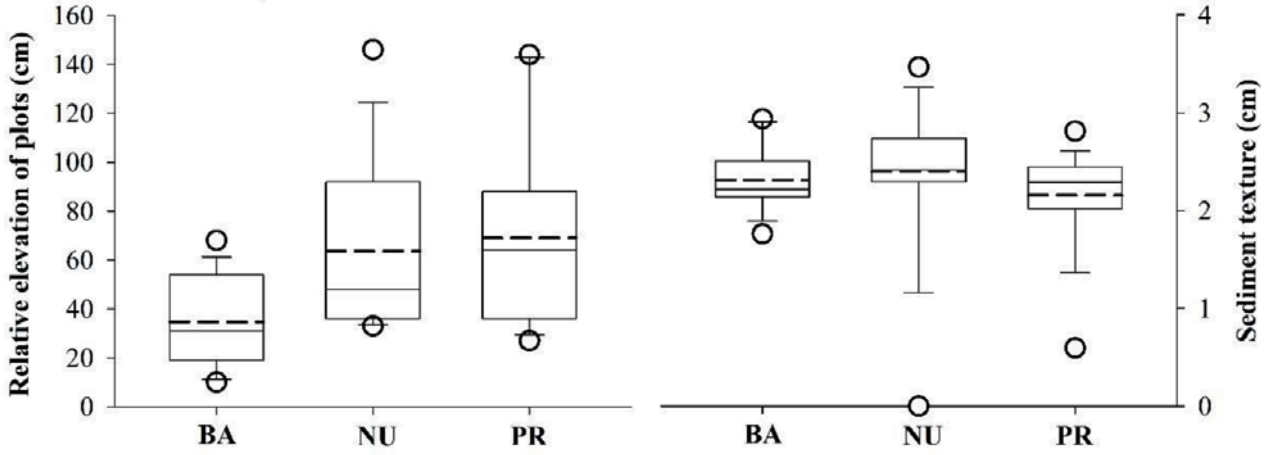

Fig. 2. Box-whiskers plots (minimum, 25%, median, mean = short-dashed line, 75%, maximum, and outliers = dots) showing variability (n=15) between rivers (BA, Baganza; NU, Nure; PR, Parma) in relative elevation of plots (left panel) and sediment texture (right panel).

annua L., *B. vulgata/frondosa* and *Euphorbia maculata* L.

The average species number *per* plot was 21.2±6.1. It peaked at BA plots, with an average value of 23.0±6.6 species, while the lowest value was recorded at PR (20.3±5.6; Fig. 3). By separating the contribution of native and alien plant species, similar patterns were observed for the native ones, with a maximum of 12.8±3.7 species *per* plot measured at BA site, and lower values for PR (12.2±4.1 species *per* plot) and NU (10.3±4.5). The latter peaked at BA and NU with similar average values (10.2 and 10.1 species *per* plot, respectively), whereas the lowest values have been recognized at PR site (with an average alien species richness of 8.1) (Fig. 3).

The cover values overlapped the species richness data trends, with an overall average value of 48.8±28.0 % per plot. The highest cover rates were recorded at BA site (64.4±34.1 %), whereas the lowest at NU site (38.4±14.7 %; Fig. 3). Both the native and alien species yielded the maximum cover values at PR site, with a clear predominance of the alien ones, with rates in the range 38.7±18.0 to 25.7±28.3 %, respectively (Fig. 3).

Concerning the mutual relationships between alien and native species richness and coverage (AR/NR and AC/NC, respectively), comparable trends were observed with the highest values recorded at NU plots for both descriptors (Fig. 4). The richness ratio (AR/NR) ranged between 0.4 and 2.0, whereas the cover ratio (AC/NC) showed values in the range of 0.22-8.80, indicating a wider variability in the cover contribution of alien species across plots and sites compared to the species richness.

Hydrogeomorphic and sediment drivers

The linear mixed models evidenced a significant effect of HT on TR, NR and AC/NC. The relation is positive in all cases, *i.e.*, we observed an increase in TR, NR and AC/NC with increasing HT (Table 2). AR was not influ-

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Tab. 1. List of the most abundant species, considering all the species with a total cumulative detection >30% (14 plots). For each *taxon*, the number of colonized plots and the mean cover values were reported, considering both the whole set of sampled rivers (Tot) and each river separately. Alien species are highlighted in bold.

	Number of colonized plots				Mean cover values			
Species	Tot	BA	NU	PR	Tot	BA	NU	PR
Xanthium italicum	**45**	**15**	**15**	**15**	**16.5**	**5.5**	**18.7**	**25.3**
Persicaria lapathifolia ssp. *lapathifolia*	45	15	15	15	6.0	3.8	1.3	12.7
Echinochloa crus-galli	42	14	14	14	2.4	2.4	2.0	2.8
Setaria italica* ssp. *viridis	**40**	**12**	**14**	**14**	**2.2**	**1.0**	**2.3**	**3.5**
Populus x canadensis	**39**	**12**	**13**	**14**	**2.4**	**1.4**	**2.4**	**3.3**
Ambrosia artemisiifolia	**36**	**15**	**15**	**6**	**10.5**	**19.3**	**2.8**	**9.5**
Bidens vulgata/frondosa	**35**	**15**	**9**	**11**	**2.4**	**1.9**	**3.2**	**2.0**
Panicum capillare	**28**	**14**	**13**	**1**	**2.6**	**1.8**	**3.5**	
Digitaria sanguinalis	**22**	**6**	**9**	**7**	**1.7**		**1.7**	
Diplotaxis tenuifolia	21	5	7	9	1.3	1.0	1.0	1.8
Persicaria lapathifolia ssp. *pallida*	21	9	4	8	1.6	2.0	1.0	1.9
Amaranthus hybridus	**20**	**7**	**0**	**13**	**2.5**			**2.5**
Chenopodium album	20	7	3	10	1.1		1.0	1.3
Polygonum arenastrum	20	10	1	9	2.0	1.6		2.4
Lysimachia arvensis	19	9	7	3	2.0		2.0	
Plantago lanceolata	19	7	6	6	1.0		1.0	1.0
Cuscuta campestris	**18**	**7**	**5**	**6**	**3.2**	**1.7**	**2.6**	**5.3**
Trigonella alba	18	0	7	11	3.0		2.5	3.5
Barbarea vulgaris	17	10	0	7	2.7	2.3		3.0
Salix alba	17	5	7	5	1.0		1.0	1.0
Amaranthus blitum	16	0	7	9	1.3		1.0	1.6
Agrostis stolonifera	15	9	1	5	2.3	3.5		1.0
Daucus carota	14	6	3	5	1.0	1.0	1.0	1.0
Euphorbia nutans	**14**	**0**	**14**	**0**	**2.9**		**2.9**	
Medicago lupulina	14	10	2	2	1.3	2.0	1.0	1.0

BA, Baganza; NU, Nure; PR, Parma.

enced by any of our explanatory variables, nor was AR/NR, although a marginally significant relationship between AR and HT was found (Tab. 2). No relation was found between ST and any of the response variables investigated.

DISCUSSION

The variation in hydrology implies changes in pioneer plant species richness at in-stream periodically exposed sediments. These results are consistent with findings from

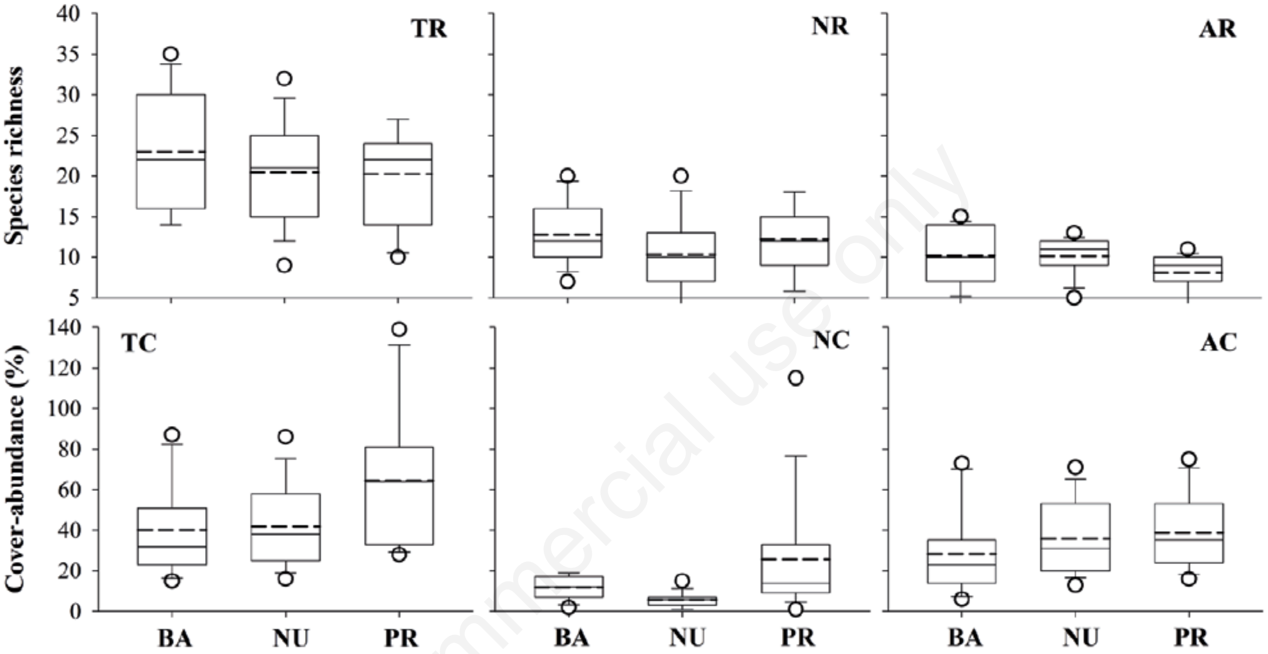

Fig. 3. Box-whiskers plots (minimum, 25%, median, mean = short-dashed line, 75%, maximum, and outliers = dots) showing variability (n=15) between rivers (BA, Baganza; NU, Nure; PR, Parma) in species richness (upper panels) and species cover (lower panels), both considering all the *taxa* combined (TR, total richness; TC, total cover), or the values for native (NR, native richness; NC, native cover) and alien (AR, alien richness; AC, alien cover) plants separately.

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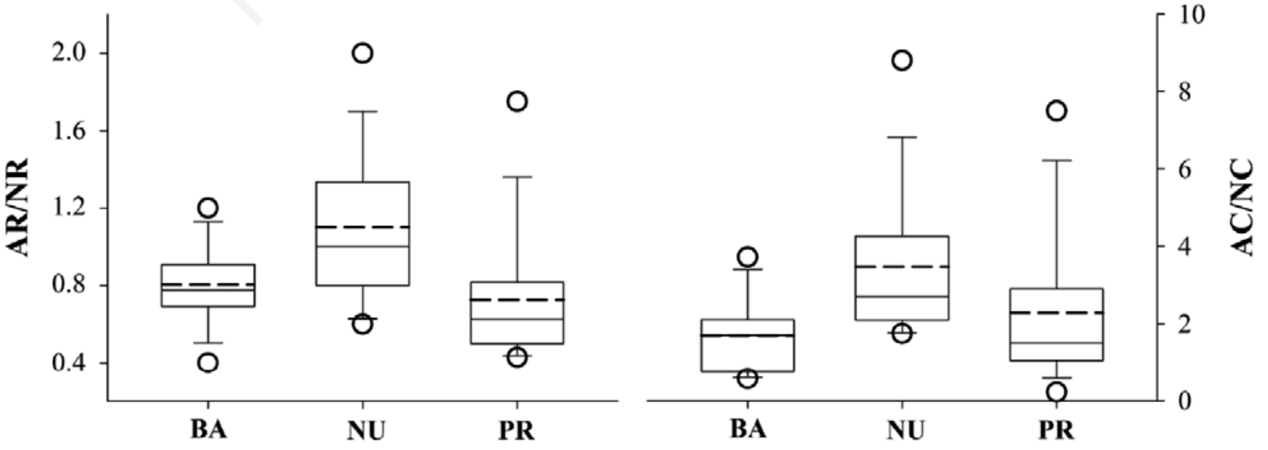

Fig. 4. Box-whiskers plots (minimum, 25%, median, mean = short-dashed line, 75%, maximum, and outliers = dots) showing variability (n=15) between rivers (BA, Baganza; NU, Nure; PR, Parma) in the ratio between alien and native species richness (AR/NR; left panel) and between alien and native species cover (AC/NC; right panel).

other studies that suggest that plants living within riparian corridors are primarily driven by climate and hydrogeomorphic disturbance, including sediment texture and cohesion (Nobis and Skórka, 2015; Gurnell *et al.*, 2016). Additionally, the structure and complexity of riparian vegetation are strictly related to the level and flow of waters and, consequently, to the saturation of substrates (Hood and Naiman 2000; Gurnell *et al.*, 2016). These factors, in turn, depend on several other factors, including the size of the watercourse, the characteristics of its longitudinal and transverse profile morphology, the prevalent uses of soil and lithology at the basin scale, as well as the groundwater-surface water interactions (Leyer, 2006; Kuglerova *et al.*, 2015; Nobis and Skórka, 2015; Gurnell *et al.*, 2016).

The present data completes these prior results widening their applicability to the plant communities typical of the riverine emerged sediments, with special reference to the contribution of hydrological disturbance in structuring the in-stream dry ephemeral vegetation. The present study suggests a progressive decrease in species richness with the increase in hydrological disturbance expressed in terms of HT level (= altitudinal arrangement of plots above water base flow) as proxy of the three-dimensional complexity of the investigated stream stretch (Tabacchi *et al.*, 1996). On the other hand, a more prolonged exposure of riverbeds may allow a greater development of pioneer plant coenoses directly associated with the establishment of a higher number of alien plants.

Indeed, a key contribution of alien species in terms of diversity has also been quantified in the studied streams, strengthening the idea of the centrality of river corridors as preeminent spreading paths for biological invasion in freshwaters and associated habitats (Lazzaro *et al.*, 2020; Bolpagni, 2021). In the present case, the increase in plant cover-abundance rates that occurs concurrently with the increase in hydrological disconnection is partly attributable to the increase in the cover rates of alien species, which are largely to be considered as ruderal species not strictly riparian (following the classification by Tabacchi *et al.*, 1996). Among these species, in fact, several *taxa* are included that are often common in agricultural and dry ruderal contexts, therefore not subject to regular flooding events [*e.g.*, *Ambrosia artemisiifolia*, *Digitaria sanguinalis* (L.) Scop., *Euphorbia nutans* Lag., *Setaria italica* ssp. *viridis*]. This suggests a progressive replacement of the plants typical of exposed riverbeds by ruderal species, only marginally adapted to the more dynamic riverbed sectors. However, this is one of the first steps towards linking the structure of pioneer riverine vegetation with its ecological determinants (*e.g.*, hydrology first and foremost) and no definitive evidence has yet been found. It seems, however, that the ruderal species richness mirrors the disturbance level within the river corridor, and in turn the degree of proximity of cultivated areas to the riverine habitats. The progressive lack of riverine ecotones boosts the spread of invaders into riverbeds from adjacent cultivated areas (Tabacchi *et al.*, 1996). Nevertheless, additional studies are needed to explore the dynamics of this kind of plants and habitats, as well as to quantify the "biotic acceptance" trajectories of in-stream plant communities.

This represents an urgent issue due to the drastic reduction in summer base-flow rates observed in several temperate regions, including the Po plain in the last decades (Datry *et al.*, 2014; Laini *et al.*, 2020; Messager *et al.*, 2021). In the presence of prolonged summer drought events, an increasing homogenization in terms of species could be expected to the advantage of ruderal plants. Indeed, the present data suggests an increase of local relevance of alien species along gradients of drought stress. However, there is only limited data indicative of the biological or functional

Tab. 2. Statistical output of the linear mixed models. p-values<0.05 are highlighted in bold, as the corresponding estimate and explanatory variable (ExpVar). The sign of the estimate value indicates the sign of the relationship between explanatory (HT, height above water base flow level; ST, surface sediment texture) and response variable (Res_var; TR, total richness; NR, native species richness; AR, alien species richness; AR/NR, ratio between alien and native species richness; AC/NC, ratio between alien and native species cover). In the model formula, (1|Site) indicates the random effect.

Res_var	Model	ExpVar	Estimate	SE	Df	t value	p-value
TR	TR ~ ST+HT + (1|Site)	ST	-4.018	3.138	37.768	-1.280	0.208
		HT	**0.091**	0.030	38.000	3.069	**0.004**
NR	NR ~ ST+HT + (1|Site)	ST	-1.802	2.011	37.598	-0.896	0.376
		HT	**0.065**	0.019	37.944	3.400	**0.002**
AR	AR ~ ST+HT + (1|Site)	ST	-2.193	1.461	37.681	-1.501	0.142
		HT	0.028	0.014	37.987	1.997	0.053
AR/NR	AR/NR ~ HT+ST + (1|Site)	HT	-0.002	0.001	37.715	-1.681	0.101
		ST	-0.098	0.151	37.320	-0.651	0.519
AC/NC	AC/NC ~ HT+ST + (1|Site)	**HT**	**0.017**	0.007	34.908	2.378	**0.023**
		ST	-0.654	0.775	37.465	-0.843	0.405

SE, standard error; Df, degrees of freedom.

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consequences mediated by the above-mentioned processes. This increases the uncertainty of global predictive models on the contribution of river networks (especially those of lowlands) to the cycles of C and nutrients at large scales (Mallast *et al.*, 2020).

Furthermore, despite the ephemeral in-stream plant communities belonging to habitats defined of community interest in the Habitat Directive 92/43/CEE, a systematic, ecological perspective for their management is largely lacking, as well as a global synthesis of the numerous local studies who investigated them, as for example Lastrucci *et al*. (2010), Angiolini *et al.* (2017), and Guareschi *et al*. (2020) for Italy. Few research, in fact, has explored their ecological determinants to integrate the analysis of their composition and structure at large biogeographical scales (Brandes, 1999; Leuschner and Ellenberg, 2017), thus reducing the possibility to draw up adequate conservation plans. For example, regarding a widely discussed principle of freshwater restoration, the ecological flow, the repercussions of hydrological regulation on dry river domains have only recently begun to be evaluated along with the increased awareness on the unique value of dry beds globally (Steward *et al.*, 2012). In this respect, the analysis of the annual "terrestrial" plants needs to be fully integrated into river monitoring programs, especially in non-perennial streams and rivers.

CONCLUSIONS

The pioneer vegetation of periodically exposed sediments plays pivotal ecological roles, representing an essential component of river ecosystems. Here, new insights on the role of hydrology and sediment quality in driving annual plant biodiversity have been offered to implement the knowledge of this neglected biological component of river ecosystems. Hydrological regulation and potential imbalances in the use of water at the basin scale may seriously affect the dynamics of this kind of plant communities, calling for the adoption of management practices that consider the ecological requirements and trajectories of the plant communities established in river corridors, not exclusively the arboreal ones. Furthermore, the present data stresses the importance of detailed monitoring studies - as well as modelling tools - on the local effects of climate change and direct human impacts to in-stream plants and vegetation dynamics. This is essential to further new or integrated eco- and hydro-geomorphological flow concepts in both regulated and unregulated rivers/basins.

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