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Perspective

Revisiting Vegetation Gradient Analysis and the Intermediate Disturbance Hypothesis for the Interpretation of Riverine Geomorphic Patterns

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Abstract: Human effects on the water economy of the river systems are currently well documented at the worldwide scale, impacting a range of ecosystem services. In this perspective article, we discuss the findings of recent papers that under different intensities of human disturbance have coupled the analyses of riverine geomorphological and plant community patterns. The discussion is carried out within the historical framework of past and current methods of sampling and analysing the river geomorphology and the plant communities along cross-sectional profiles. The research has been conducted along three major gravel-bed rivers of the south-eastern Italian Alps: Brenta, Piave, and Tagliamento. The collated and summarised results here demonstrate the existence of a strong relationship between the woody species variance that can be explained by geomorphologic patterns and human disturbance intensity. The less disturbed river has an intermediate value of species variance that can be explained by geomorphology, the intermediate-disturbed river has the highest value, and the highly disturbed river has the lowest value. Then, we proposed an interpretation key and an adaptation of the intermediate disturbance hypothesis, which reads as: "in rivers, the greatest influence of geomorphic properties on vegetation occurs in the moderate or middle ranges of a human disturbance gradient". We argue that the "influence of the geomorphic properties on vegetation" is assessed through the species constrained variance through an ordination analysis, such as that which is explained here. The most recent collection techniques based on field survey and remote sensing are making it increasingly easy and accurate to study of the trends of geomorphic and plant community variables throughout time and space. Thus, we encourage that researchers should check whether and how our observation is conserved through different groups of taxa and intensities of natural and human disturbance.

Keywords: geomorphological processes; riverine vegetation; human interference; intermediate disturbance hypothesis

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1. Introduction

The human pressure on the water economy of river systems is well documented at the worldwide scale, impacting a range of ecosystem services [1]. Human pressure on rivers ecosystems is historical and long lasting in Europe due to the long legacy of land use. From the late Bronze age onwards, agricultural activities, forest opening, and grazing in woodlands have changed the landscape mosaic [2]. For example, the effects on soil nutrient availability, increased erosion, and the loss of plant biodiversity driven by agriculture in the Roman period can still be traced today [3]. Increased soil erosion due to land use changes is regarded as the main cause of river sediment deposition, which is considered to be one of the most important geomorphic trends in the Holocene. Land denudation makes the land more susceptible to soil erosion during extreme rainfall events, especially in the context of climate change. In Europe, successive periods of woodland clearance, cultivation, and abandonment produced fluctuations in the sediment inputs to rivers [4]. In the modern day, European forests have reached their minimum extension around the middle of nineteenth century, as they were exploited for fuel and construction material. Rivers were used as transport routes of goods and wood, in rafts or as loose logs, and this also caused rivers to be modified to optimize the transport of logs [5]. However, in more recent times, due to economic, industrial, and demographic changes and improved logging techniques, the sizes of the forested areas in Europe began to increase again. Broadleaved conversion to conifer forests, artificial afforestation, conversion from coppice to high forests have been among the most influential recent changes in forest management [6]. Agricultural marginal lands have been abandoned, and they were spontaneously covered by secondary woodlands within a few decades [7].

As for the land, the natural courses of rivers have been frequently rectified and channelised in an attempt to reduce the risk of flooding to facilitate water abstraction and to reclaim land for agriculture. Over the past two centuries, the construction of hydroelectric power plants has also caused alterations in the water and sediment fluxes, resulting in severe hydrological morphological changes. Lastly, the need for materials for conduction in a context of economic development has increased aggregate mining activity in streams [8]. Channelisation, embankments, sediment entrapment by dams, the evolution of agriculture, industrialisation, and urbanization have produced changes in the catchment and river networks that have resulted in severely affected sediment budgets in terms of catchment [9]. All of these human activities have affected severely the natural river hydrodynamic and geomorphic features, reducing their ecosystem services. In turn, these have produced changes in the riverine vegetation composition and structure [10].

Changes in rivers due to human pressure have been traditionally studied with a focus on water and sediment fluxes [11]. More recently, the hydromorphological nature of rivers has received more attention. Although earlier studies about the human impacts on riparian plant communities have focused on single species distribution and ecology, new disciplines such as plant sociology and phytosociological science, which was founded one century ago, have helped our understanding of vegetation dynamics in riverine areas [12].

Along with this progress, river management has focused mainly on engineered structures because water management authorities have commonly seen river vegetation as an impediment to be controlled or removed. More recently, integrated approaches have been developed, aiming at describing the relationship between the river processes, human impact, vegetation, and geomorphological features [13].

Geomorphological changes have been widely studied in gravel-bed rivers in different geographical settings with different intensities of human pressure. This attention is due to the extensive volumes of extracted sediment in gravel-bed rivers that are mostly located in densely populated regions and where riparian vegetation is severely affected [14]. Hence, studying the historical evolution of riverine physical and biological factors is useful for planning sustainable river management strategies. Indeed, it is also interesting to compare rivers that differ in their distances from the potential natural conditions and in the intensities of human influence. This comparison is important because an area being wilder does not necessarily imply that it has a higher degree of biodiversity [15]. The intermediate disturbance hypothesis suggests that at the intermediate levels of disturbances, communities show a higher number of species [16]; in other words: “the greatest diversity occurs in the moderate or middle ranges of a physical gradient” [17]. The general rule predicts peaks in diversity at the intermediate disturbance levels: humped (∩) diversity–disturbance relationships. This hypothesis has been criticised and revised since non-linearities and non-additivities are now more frequently observed, particularly when the disturbances are natural [18,19].

An important opportunity for comparing the relationship between human pressure and riverine vegetation and testing the intermediate disturbance hypothesis is provided by the occurrence of three major gravel-bed rivers draining the southern-eastern Alps, namely the Brenta, Piave, and Tagliamento. These rivers are comparable in terms of catchment area, potential geomorphic settings, and climatic conditions. However, they differ in the historical and current land uses, which directly and indirectly impacted or are currently impacting their watercourse [20].

In this perspective we briefly describe the historical evolution of the human uses of the three rivers and explore the observed changes by applying an integrated ecological and geomorphological approach to consider the effects on the vegetation and river features. We also describe the evolution in survey and sampling techniques, from the earlier ones to the more recent integration with remote-sensed data. Then, we apply and recommend a survey, sampling, and analytical approach to test the intermediate disturbance hypothesis, which could be replicated elsewhere. Based on this experience, we propose a future scenario for the better integration between vegetation and geomorphological studies in rivers.

2. Setting the Scene: South-Eastern Alpine Region

2.1. The Main Geographical and Environmental Patterns

The study area is located in the south-eastern Alps and, more precisely, in the Venetian and the Friulian Pre-Alps and their subalpine hills [21]. In this area, the Brenta, Piave, and Tagliamento Rivers have a braided form, while their upper unicursal course is in the Dolomites and the Carnic and Julian Alps.

The Venetian Pre-Alps are composed of a series of mountain groups, with the highest altitudes being around 1700–2250 m. a.s.l., which have been partially configured as high plains and long tracts that are distinctly separated in the Alpine region by large longitudinal valleys (Valsugana and Valbelluna). Making a uniform description of the landscape of this region is hard because the soils are variable, but the geology is mainly calcareous, and it is of different ages, with rock types ranging from dolomitic to marlstone. This composition includes karst phenomena, caves, and a scarcity of superficial water bodies. Above 800 m. a.s.l., vast, high plains (Asiago, Cansiglio, and Lessini) prevail here and there, interrupted by rocky dolomitic groups (Pasubio). Glacial forms are uncommon and not striking. The pre-alpine groups are interrupted and bordered by deep valleys and steep slopes, which mark a striking limit with the flatland. Due to the harshness of these slopes, the cultivation of food crops (i.e., of potatoes, cereals, vegetables, and orchards) is scarce and often abandoned. Woodlands are widespread throughout the whole of the region. Conifers and pastures are common at the highest altitude, while broadleaved trees cover the foothills.

The subalpine hills, which are fragmented and heterogeneous, are the foot of the pre-Alps. They emerge (200–300 m. a.s.l.) from the flatland as independent ranges in bumps or parallel ridges, according to their geological constitution with Cenozoic soils that lean towards the plain. They are interrupted or separated from the Pre-Alps by the alluvial flatland. The hills are densely covered by broadleaved trees and with vineyards, cereals, and orchards. Settlements and industrial districts are common.

The Brenta River (174 km-long) has a basin of 2300 km^2, it is mainly pre-alpine, it originates from the Lévico and Caldonazzo lakes at 440 m. a.s.l., and it has a low slope. It runs in the Valsugana, and after receiving water from the Cismon torrent, it flows in the flatland at Bassano del Grappa, flowing within artificial embankments into the Venice lagoon, which is south of Chioggia.

The Piave River (220 km-long) has a basin of 4100 km^2, and it is mainly in the Carnic and Belluno Pre-Alps in the south and the Dolomitic Alps in the north. It originates at 2037 m a.s.l. on Mt. Peralba. It crosses the Comélico and Cadore valleys, receiving water from the Ansiei and Boite torrents, and it forms an artificial basin in Pieve di Cadore, then it flows towards Ponte nelle Alpi, and downstream of Belluno, it receives water from the Cordevole torrent. When it flows in the flatland, it leads south-east with a wide, braided channel in the high flatland, which narrows again in the artificially embanked lower flatland.

The Tagliamento River (172 km-long) drains an area of 2600 km^2, receiving almost all of the waters from the Carnic Alps. Its sources are at Mauria Pass (1195 m a.s.l.), which is between Carnia and Cadore, and it flows before longitudinally towards the east until it reaches a confluence with the Fella River, then, southward to the sea, where it flows between the Marano and the Caorle lagoons. Its channel is wide in the flatland, with a huge network of braids, which become dry near Codroipo. In the final reach, the river narrows and flows into the sea through an estuary.

The climate is transitional between the alpine and the northern Adriatic. The Alps are a peculiar geomorphological feature, and they have effects on the snow accumulation, tropospheric air circulation, and wind regimes. The influence of the sea is marked in mitigating temperature extremes, increasing air moisture, and causing heavy precipitation. Annual rainfall is particularly high north of the high Venetian plain, 1500–2800 mm, with relatively frequent storms. The minimum amount of rainfall occurs in winter, with two peaks in spring and autumn. The mean annual temperature is between 16 °C and 12 °C. Frost is rare.

2.2. Floodplain Vegetation

The riparian vegetation occupying the studied reaches is azonal. It is represented by the same plant communities in all of the study areas because they are determined by the same extreme soil factors that are dependent on the water discharge that overrule the effects of climate. A cross-section through the complete series of floodplain vegetation is represented in Figure 1.

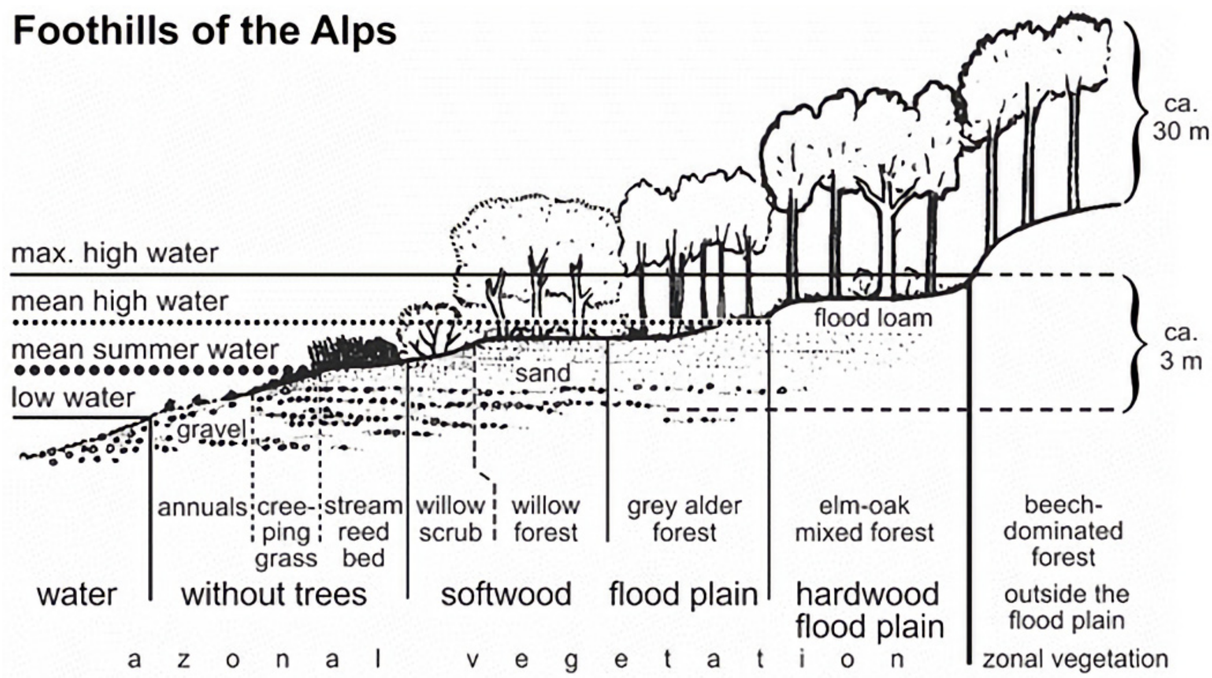

Figure 1. A schematic profile through a series of floodplain plant communities (from [22]).

The riverbanks are frequently inundated, but sometimes they are very dry for long periods, and they are colonised by herbaceous pioneer annual plants (*Chenopodium* and *Polygonum*). Perennial tall grasses and reeds grow when inundation is infrequent. Riverside willow scrub with *Salix purpurea* and *S. triandra* usually forms a narrow strip along low gravel or sand banks, which are replaced by the often flooded riverside woodlands of *S. alba* (white willow) and *Alnus incana* (grey alder). Hardwood woodlands dominated by

Fraxinus (ash) and other tree species (e.g., elm and oak) cover areas with fertile soil that are only unusually flooded.

From a morphological point of view, the description and characterization are based on the elevation above the bottom of the flowing channel (thalweg). Low bars are those areas that are frequently inundated because of their low elevation above the thalweg, whereas high bars are those areas placed at higher elevation where the inundations happen less frequently. Outside the active channel, there is the floodplain, which is higher than the thalweg is and is flooded only during flood events with recurrence interval of longer than 1.5–2 years.

The above descriptions are schematic approximations because the series of plant communities are never as clear and stable as it appears to be. Such representations help us to understand the habitat conditions that the river can change through erosion, sedimentation, and lateral shifts. However, the availability of multiple aerial imageries and highly accurate remotely sensed data, coupled with the high-resolution sampling of vegetation, have introduced new interpretative tools, which we present in the next section.

2.3. Historical Trends in Land Use and Their Effects on Morphological Dynamics

The human presence within river catchments has produced indirect impacts on the morphodynamic and vegetation patterns of rivers. These impacts, combined with the direct ones, associated with gravel mining, infrastructure, water abstraction and embankments have changed their morphometry and morphodynamics, generally resulting in a more stable and simplified river morphologies. Here, we focus on the major impacts produced during contemporary periods. As mentioned in the introduction, the effects of recent pressures are hardly separable from the long-lasting ones.

Of the three rivers, the Brenta has been, without a doubt the most impacted one. The pattern of its morphologic features has changed from braided to wandering [23] due to a considerable lack of sediment availability after the extensive building of check dams, dams, embankments, and gravel mining, which have caused incision and narrowing between the 1950s and 1980s. Therefore, bank erosion due to local sources has depleted most of the sediment [24]. The recent prohibition of gravel mining has started a new process of equilibration between widening and narrowing [23].

The Piave River is experiencing the most complex effect of human pressure. Hydroelectric dams, flow diversions, gravel mining, and stream bank protection measures have greatly reduced the channel's width and braiding [25], increasing the islands' proportions [26]. The downstream variability of grain size does not follow a simple decreasing pattern, but it is discontinuous due to a mixture of natural and anthropogenic factors [27]. Where the morphological patterns have shifted from braided to wandering, the former active channel is covered by riparian vegetation [26].

The Tagliamento River is regarded as a reference natural system because of its unconfined floodplain segments, mosaic of aquatic and terrestrial habitats, many vegetated islands [28], exposed gravel bars, and large stores of wood [29], realization of the shifting mosaic steady-state model [30], and highly morphodynamic properties [31]. However, human impacts on the Tagliamento River are well documented, such as incision and narrowing along some reaches due to stream embankment and urbanization [32].

In general, the channel adjustment trajectories of the reaches that are studied here can be represented in Figure 2, which was inspired by the classification of Surian et al. [33]. Brenta followed its trajectory from I to III and that of Piave from I to II, while Tagliamento belongs still to pattern I. The difference in the channel adjustment trajectories here described justifies the interest of comparing the three rivers for the relationships between the morphological features and vegetation.

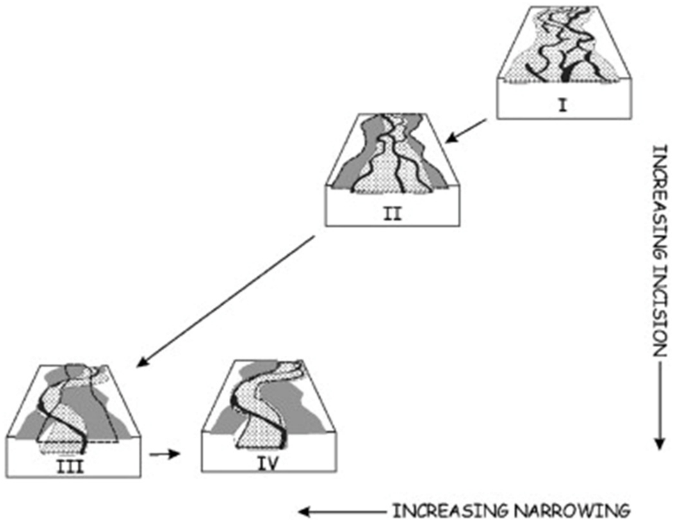

Figure 2. Schematic diagram of the morphological dynamic which is happening in the studied rivers (from [26]). Dotted areas represent the river channel, while grey colour represents the abandoned areas. The four patterns from I to IV represent four subsequent stages of river morphological dynamic in the Brenta, Piave, and Tagliamento Rivers from the early nineteenth or the twentieth centuries (pattern I) to the present-day morphology (pattern IV).

3. Riverine Morphodynamic and Vegetation Patterns

3.1. Scientific and Technical Progress in the Theoretical and Conceptual Framework

Vegetation patterns can be described at several resolutions, levels, and using a variety of classification schemes. The occurrence and abundance of single plant species dominated early reports, but they have been later represented by the grouping of individual plant communities by their floristic similarities, an approach that was chosen for phytosociological classification [34]. The spectrum of vegetation types may also be analysed along the gradients of environmental factors, species populations, and community characteristics by performing a gradient analysis of the vegetation, which are defined directly when the samples are taken from single environmental transects at equal intervals. The community characteristics may include measures such as species diversity, canopy cover, and annual production [35] (Figure 3).

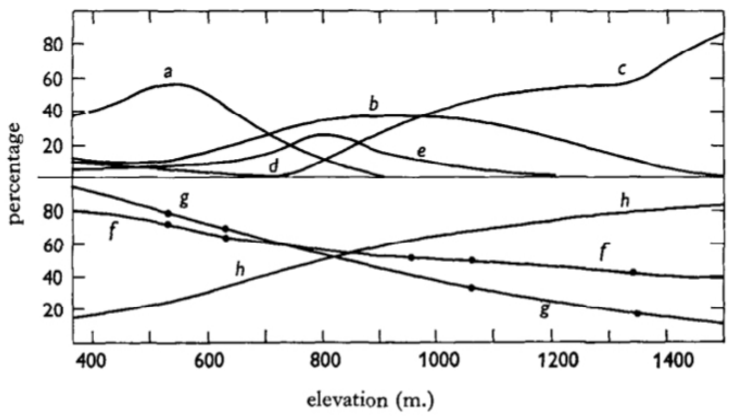

Figure 3. A direct gradient analysis along an altitudinal gradient (from [35]). Results belong to a vegetation study from Tennessee, in which samples are grouped by intervals of 100 m of elevation. The upper part of the figure shows the tree species (letter a–e), while the lower part of the figure shows the community characteristics (letters f–h). a: *Pinus virginiana*; b: *P. rigida*; c: *P. pungens*; d: *Quercus marilandica*; e: *Q. coccinea*; f: species diversity of all vascular plant strata in sample quadrats; g: tree stratum above-ground net annual production; h: coverage of the predominantly ericaceous shrub stratum.

This type of direct gradient analysis is appropriate to study how riverine vegetation changes along the environmental gradient from the alluvial flatland to the flowing channel. The representation of the gradient is traditionally achieved with curves fitted to a measure of the species population against values of one or more environmental factors [36]. Ideally, the environmental factor should be associated with many factors of environmental complexes, which change concomitantly. Figure 1 is a simplified version of one curve, which represents the dominant plant species and their heights, plotted against the elevation above the thalweg.

Here, we focus on the part of the environmental heterogeneity of the riparian corridor that extends laterally, although heterogeneities exist also vertically, longitudinally, and as a dynamic mosaic of patches associated with multiple spatial and temporal geomorphological scales [37].

The geomorphological adjustments we described in the previous section generate lateral and vertical changes within the active channel and a dynamic series of vegetation assemblages. Canopy structure and composition are strongly associated with stand age and their horizontal and vertical position along the river corridor. The ecological spectrum of the herbaceous communities follows a similar pattern. The dynamic aspect of this lateral heterogeneity cannot be described with traditional cross-sections. The solution is to find the correspondence between the stand age and the horizontal location by using stand age as a proxy of the relative lateral position, such as in Table 1; one of the earliest examples of vegetation gradient analysis focused on river geomorphic patterns. Johnson et al. [38] also related stand age to tree species diversity and variety, the soil texture, and nutrients.

Table 1. Correspondence between relative stand age and lateral position on the floodplain in the Missouri River. Values are percentage cover of stands (from [38], modified).

	Stand Age Class		
Zone	**Young**	**Medium**	**Old**
Center	64	18	8
Intermediate	36	73	25
Edge	0	9	67

Another example is given below (Figure 4), where the cross-section has been improved, indicating the geomorphic features associated with specific values of flow frequency and duration and those related to the dominant tree species [39].

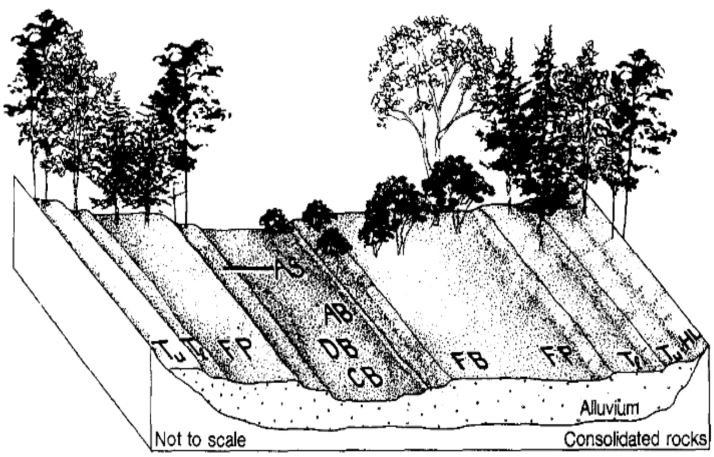

Figure 4. Fluvial geomorphic and vegetative characteristics (AB = channel-shelf bank, AS = channel shelf, CB = channel bed, DB = depositional bar, FB = bank below the floodplain, FP = floodplain, HL = hillslope, T_l = lower terrace, and T_u = upper terrace) (from [39]).

Using phytosociological approaches, very detailed series of plant communities along the lateral transect (perpendicular to the river) have been published for many rivers [40,41]. They are more precise than the previous examples because they refer to specific reaches. Some of them have been prepared from the three rivers that are studied here, for example, Figure 5 below shows a cross-section along the middle course of the Tagliamento River.

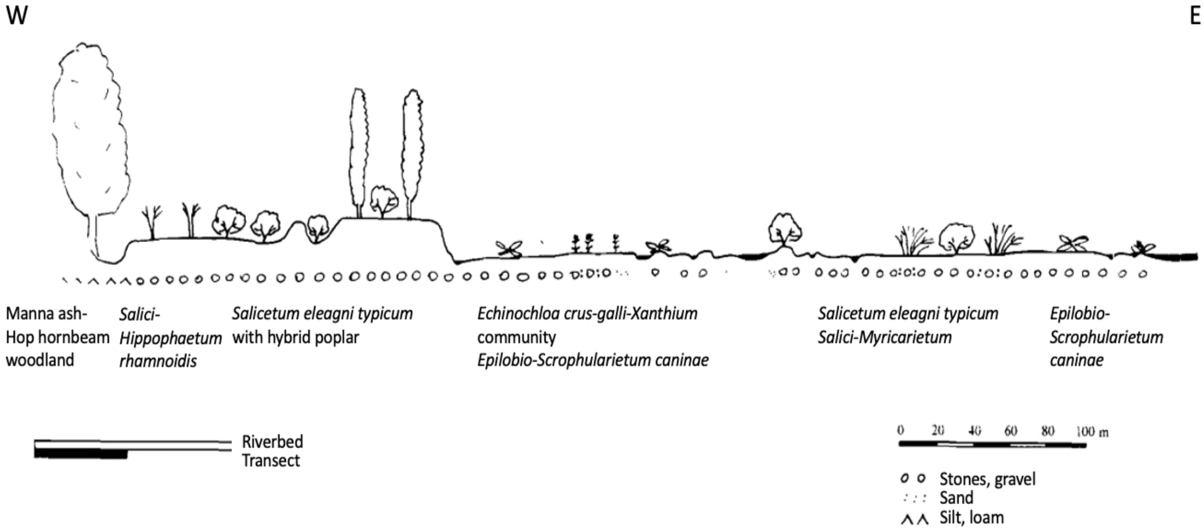

Figure 5. A cross-section of plant communities along the middle course of the Tagliamento River (W–E orientation) (from [42]).

We could show many others for other Italian rivers including the rivers that are studied here. The purpose of them is to analyse the relationships between the plant communities associated with the geomorphologic units and soil properties of distinct reaches of a watercourse, with the final aim to describe different river units (geoseries or geosygmeta). These will serve as predictive models to manage watercourses and conserve their biodiversity [40].

The replicability of these observations can be achieved by integrating them with a sampling design, as a gradient analysis implies. Belt transects, which are perpendicular to the active channel, are taken through the entire river corridor, from terrace to terrace. The choice of the site location, the number of segments, the width, and the nesting of subsamples are part of the sampling design, as well as how and what measure in the community and in the environmental characteristics. The relationships between the two groups of variables (community and environment) are commonly evaluated by using group comparisons (using ANOVA and *t*-test methods), ordination, or simple regression, or a mixture of them; for example, by calculating the correlation coefficients of the environmental variables with the ordination axes of species composition patterns [37,43].

These types of analyses may be still combined with drawing representative cross-sections. For example, high-resolution cross-sections have been produced (Figure 6) by grouping the sampling units into clusters with similar plant compositions, and profiles have been drawn at scales that are proportional to the soil layers depth [44].

Recent remote sensing, positioning, and geographic techniques, such as aerial borne laser scanners (LiDAR), differential GPS (DGPS), and geospatial imagery analysis and processing, have greatly revitalised the interest in gradient analyses. It is easier today than it was in the past to replicate sampling and to obtain accurate and precise values of community and geomorphic variables. In the next section, we will show how the authors cooperated in the three case studies that are presented.

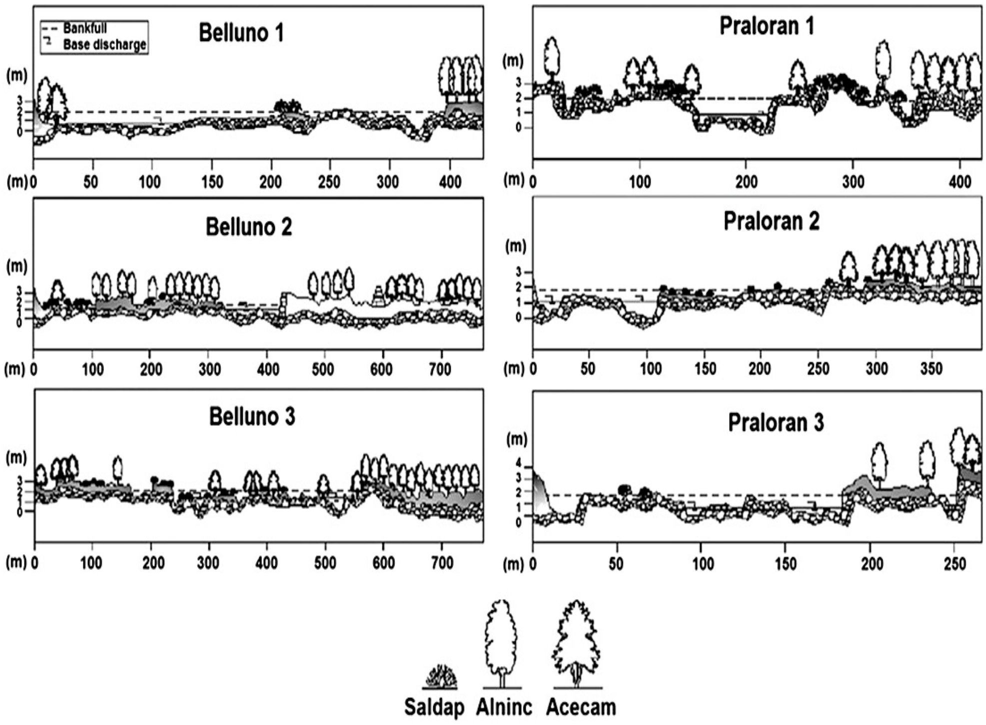

Figure 6. Cross-sections of plant communities in six sub-reaches of the Piave River. The left side of all of the images correspond to the left bank (Alninc: *Alnion incanae*; Acecam: *Rhamno-Prunetea*; Saldap: *Salicion* eleagni). Symbols of trees are not to scale (from [44]).

3.2. Overlook on the Methods Used and Our Experience with Testing the Intermediate Disturbance Hypothesis

The study of the three rivers is particularly promising as they are all potentially braided. However, because of the different levels of human pressure which they have been exposed to in recent decades, they currently also show wandering geomorphologic patterns, and they differ from the natural references, although to different degrees.

Here, we present and analyse a vegetation gradient that was surveyed through lateral transects. Each transect, taken along the full river corridor width, was divided into equally sized contiguous plots with 4 m sides, and they were spaced 10 m apart from each other. The transect length ranged from 266 to 1000 m. We surveyed 710 sampling units (at least 35 units for each sub-reach).

We emphasise that this type of analysis requires the concomitant collection of data on the environmental variables, species populations, and community characteristics. In this case, the environmental variables included are: the elevation above the thalweg, the thickness of the fine sediment layer, the grain size distribution, and geomorphic persistence. The elevation above the thalweg was measured using a DGPS. The river bed is composed of different sedimentary layers depending on the different flood intensities and on the type of sediment transport during these events [45]. Therefore, the depth of the different sediment layers is an indicator of the most recent sediment transport phases that occurred during recent floods [46]. Grain size distribution was calculated as the D_{50} of 30 randomly selected grains.

Geomorphic units are the elementary spatial physical components of a river, as part of the fluvial dynamics, and they also represent habitats for biological organisms [47]. We identified three types of geomorphic units: floodplains, islands, and bars. The task of individual sampling units to a geomorphic type was conducted through a visual assessment. From the aerial photos, we identified the geomorphic units at different times to assess the persistence of the geomorphic unit, a proxy of the most recent changes that occurred [48].

Figure 7 shows the distribution of 18 lateral transects that were surveyed in 2010 along the Brenta, Piave, and Tagliamento Rivers. It also shows the main geomorphic patterns (i.e., the frequency of geomorphic types and the width of the active channel).

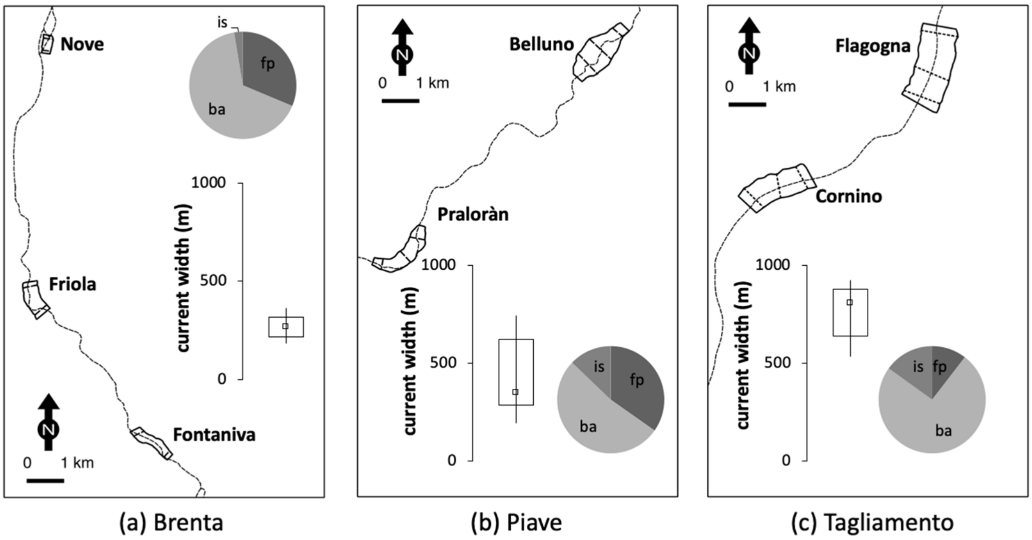

Figure 7. The studied sub-reaches, frequency of geomorphic types (fp: floodplain; ba: bar; is: island) in the plots, and the current width of the active channel (box and whisker plots) (from [20]).

In potentially braided rivers, there is a close negative correlation between the proportion of islands, the width of the channel, and its anthropogenic character [49]. In fact, the Brenta River is more human impacted than the other two are, and it has a low island portion, as well as a smaller active channel width.

We sampled communities of woody species. The woody species were surveyed in 2010 in all of the sampling units: 393 of them had at least 1 woody species. The community characteristics included the trees' diameters and heights.

Three plant communities characterised by tree species have been identified through the cluster analysis. An indicator species analysis was used to assess the exclusiveness for a tree species in one or more groups. Each sampling unit was assigned to a plant community. The most natural river (Tagliamento) is the richest in indicator species, and the other two follow in order of the degree of human disturbance, contradicting the theory behind the intermediate disturbance hypothesis [50].

The relationships between the species occurrence from the set of sampled units and the classification of the same units into groups can be analysed in different ways. An ordination analysis is a solution which aims to outline the gradients. Species, which are characterised through their presence in multiple sampling units (multivariate objects), are ordered to have species with similar occurrence patterns near each other, and the species with dissimilar patterns are farther from each other. Community and geomorphic variables can be treated as explanatory variables of the patterns. A redundancy analysis (RDA) is a type of direct gradient analysis that aims to summarise the linear relationships between the components of the response variables (occurrence of species) that are explained by a set of explanatory variables (geomorphic and community characteristics). It can be considered a constrained version of the principal component analysis (PCA) [51].

RDA ordination may be presented as a biplot (Figure 8), where the objects are points (light grey) and either the response or explanatory variables are vectors (arrows). The direction of the vector is the direction of the increase for that variable. Levels of nominal variables (rivers and species) are plotted as points (dark grey) (Figure 8A), and they show the average position of the sites that belong to one river or contain a particular species. Several types of scaling are possible. In our example (Figure 9), we did not plot sampling units (objects), and the angles between all of the vectors reflect their (linear) correlation

(Figure 8B). Projecting centroid points (dark grey points) representing species or rivers onto a vector (arrows) representing a geomorphic or community variable reflects the relationship between these variables.

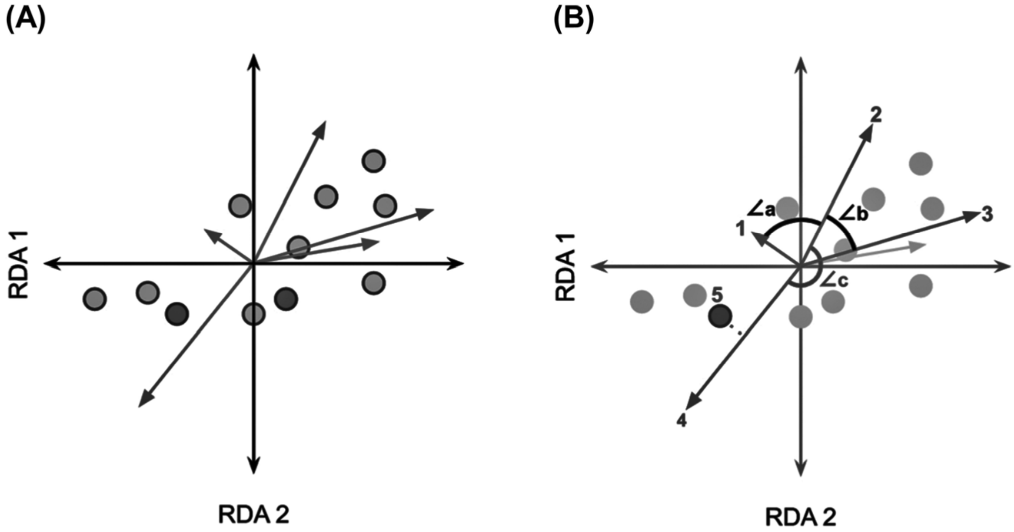

Figure 8. (**A**) Schematic representation of a RDA ordination biplot, where objects are points (light grey), and either the response or explanatory variables are vectors (arrows). Levels of nominal variables are plotted as points (dark grey) (**B**) In our example, the cosines of angles between vectors (**B**) approximate the correlation between the variables they represent. In this case, ∠a is approaching 90°, which suggests that variables "1" and "2" show very little correlation (they are almost orthogonal, just as independent axes are). ∠b is less than 90°, suggesting positive correlation between variables "2" and "3", while ∠c is approaching 180°, suggesting strong negative correlation between variables "2" and "4" (the directions of increase for variables "2" and "4" oppose one another). Variable 5 is non-quantitative, and it is represented by a centroid. A right-angled projection onto variable 4 suggests the two variables are positively linked (from [52], modfied).

The overall RDA solution and each axis have their significance values, and the variance explained by the explanatory variables that can be quantified using statistical software. Here, we used several packages of the R software [53].

We produced an RDA biplot of our case study (Figure 9). The explanatory quantitative variables are represented as vectors. The rivers, which are nominal variables, are represented as different symbols with increasing size, representing the increasing anthropogenic disturbance. The species are represented with their centroids. The overall RDA solution and all of the axes are significant, and 30% of the variation in the species patterns is explained by the variation in the explanatory variables.

It is evident how the sites belonging to most disturbed Brenta River are mostly characterised by a lower number of species and by higher soil grain size, no matter which geomorphic type is considered. The fact that the Brenta River is associated with *Berberis vulgaris*, a flood-intolerant species that is naturally relegated to high terraces, is an indication of human influence on the flood dynamic [54]. Interestingly, geomorphic persistence is not correlated to high species richness. The other geomorphic variables are correlated with each other, and they are also correlated with community characteristics. The Piave River floodplain is the more persistent, and it is associated more than other floodplains are to *Fraxinus oxycarpa*, a tree species that is restricted to swamps, rivers, or temporarily flooded depressions in the alluvial plain [55]. It is difficult from the biplot to discern the specific associations of species to a single geomorphic type, as expected from azonal vegetation.

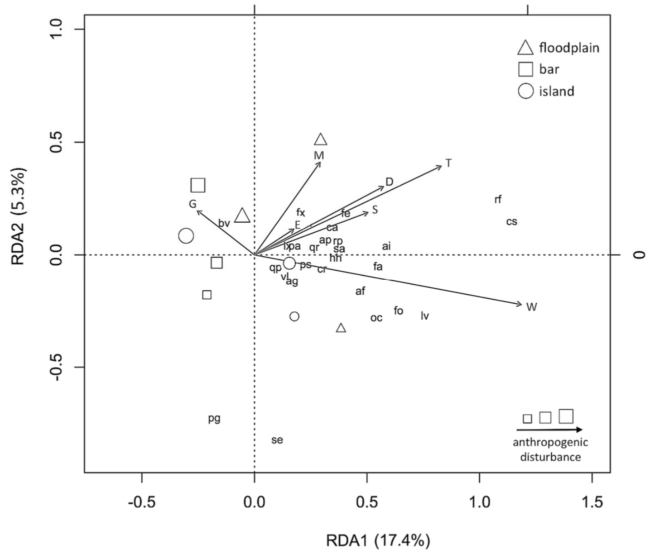

Figure 9. RDA ordination biplot of the observations on 234 plots. Arrows represent the biplot scores of environmental and stand variables (G: grain size; M: geomorphic persistence; E: elevation above thalweg; D: mean DBH; T: mean tree age; S: fine sediment; W: number of woody species). The centroids of the combinations of river and geomorphic types are denoted by plan figures with sizes that are proportional to increasing intensity of anthropogenic disturbance (Tagliamento < Piave < Brenta) and variable shapes depending on the geomorphic type. Lowercase codes are the species with goodness-of-fit > 15% (af: *Amorpha fruticosa*; ag: *Alnus glutinosa*; ai: *Alnus incana*; ap: *Acer pseudoplatanus*; bv: *Berberis vulgaris*; ca: *Corylus avellana*; cs: *Cornus sanguinea*; fa: *Frangula alnus*; fe: *Fraxinus excelsior*; fo: *Fraxinus ornus*; fx: *Fraxinus oxycarpa*; hh: *Hedera helix*; lx: *Lonicera xylosteum*; lv: *Ligustrum vulgare*; oc: *Ostrya carpinifolia*; pa: *Picea abies*; pg: *Populus nigra*; ps: *Pinus sylvestris*; qp: *Quercus pubescens*; qr: *Quercus robur*; rf: *Rubus caesius*; rp: *Robinia pseudoacacia*; sa: *Salix alba*; se: *Salix eleagnos*; vl: *Viburnum lantana*) (from [20]).

However, by performing three separate RDA analyses, one for each river, the amount of species variance explained (constrained) by the geomorphic variables, though this is always significant, is higher in Piave River than it is in the Tagliamento and Brenta Rivers (Figure 10).

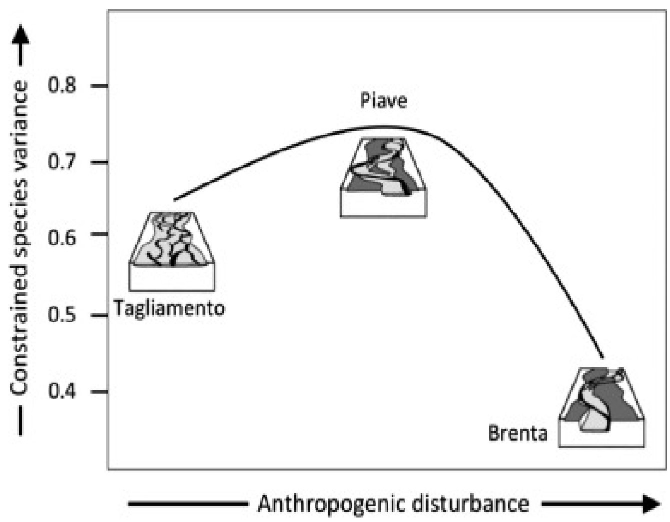

Figure 10. Schematic diagram showing how the variance of woody species explained by geomorphologic patterns increases passing from the Tagliamento River to the intermediately disturbed Piave River, and then reduces again to the lowest level in the highly disturbed Brenta River (from [20]).

The relationship observed in the diagram above is similar to the well-known humped diagram representing the intermediate disturbance hypothesis theory and its corresponding rule.

4. Concluding Remarks

Using equally spaced and sized sampling units in lateral transects is a way to study the relationships between geomorphic and plant community properties. This type of analysis is traditionally called vegetation direct gradient analysis because it combines the collection of environmental factors, species populations, and community characteristics using a gradient of one or more environmental factors.

Riverine vegetation gradient analysis has been traditionally focused on accurate plant community studies. In recent decades, this has been combined with the study of geomorphic variables. The availability of precise and accurate collection techniques based on the GIS environment, allows researchers to study the trends of geomorphic and plant community variables throughout time and space. We have shown some examples of diagrams, tables, and statistical techniques that can assist researchers in the interpretation of gradients.

The river vegetation gradient analysis of lateral transects can be used to test the classical intermediate disturbance hypothesis. Here, instead of stressing the focus on diversity by itself, we were more interested in the portion of species community variance explained by the geomorphic properties. We found a strong relationship between that portion and the human disturbance degree because the less disturbed Tagliamento River had an intermediate value of species variance which could be explained by the geomorphology, the intermediate-disturbed Piave River the highest one, and the highly disturbed Brenta River the lowest one.

This is only one example of the potential of applying the same sampling design to several rivers. By using the case study of the three rivers, we can propose an interpretation that is key to the adaptation of the intermediate disturbance hypothesis, which reads as: "in rivers, the greatest influence of the geomorphic properties on vegetation occurs in the moderate or middle range of a human disturbance gradient".

Further research on other rivers will enable researchers to test this key interpretation by using different taxonomic groups and different levels of natural and human disturbance. Finally, we propose that the "influence of geomorphic properties on vegetation" is assessed through the variance value that is here explained.

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