Citation for published version (APA):
Understanding processes of island development on an island braided river over timescales from days to decades

<table>
<thead>
<tr>
<th>Journal:</th>
<th>Earth Surface Processes and Landforms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manuscript ID</td>
<td>ESP-17-0489.R2</td>
</tr>
<tr>
<td>Wiley - Manuscript type:</td>
<td>Special Issue Paper</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>n/a</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Gurnell, Angela; Queen Mary, University of London, Geography Bertoldi, Walter; Universita degli Studi di Trento, Ingegneria Civile Ambientale e Meccanica Francis, Robert; King's College London, Geography Gurnell, John; Queen Mary, University of London, Biological and Chemical Sciences Mardhiah, Ulfah; Freie Universität Berlin, Institut für Biologie, Plant Ecology</td>
</tr>
<tr>
<td>Keywords:</td>
<td>river islands, biogeomorphology, fluvial processes, riparian vegetation, wind</td>
</tr>
</tbody>
</table>
Understanding processes of island development on an island braided river over timescales from days to decades

Angela M. Gurnell, Walter Bertoldi, Robert A. Francis, John Gurnell, Ulfah Mardhiah

Bar colonization by vegetation and subsequent island formation is a key biogeomorphological process in fluvial landscape evolution. We investigate morphological and ecological evolution of river islands over timescales from single floods to decades. We show that it depends on the frequency-magnitude of sediment-seed delivery and redistribution by flood and possibly wind events and the ability of establishing vegetation to retain this material, which in the short-term may vary with seasonal to annual moisture supply, substrate characteristics and climatic growth conditions.
Understanding processes of island development on an island braided river over timescales from days to decades

Short title: Understanding processes of island development

Angela M. Gurnell\(^1\), Walter Bertoldi\(^2\), Robert A. Francis\(^3\), John Gurnell\(^4\), Ulfah Mardhiah\(^5,6\)

\(^1\) School of Geography, Queen Mary University of London, Mile End Road, London E1 4NS, United Kingdom.

\(^2\) Department of Civil, Environmental and Mechanical Engineering, University of Trento, Via Mesiano 77, 38123 Trento, Italy

\(^3\) Department of Geography, King's College London, Strand Campus, London WC2R 2LS, United Kingdom

\(^4\) School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, United Kingdom.

\(^5\) Institut für Biologie, Plant Ecology, Freie Universität Berlin, Altensteinstr. 6, D-14195, Berlin, Germany


* Corresponding author: a.m.gurnell@qmul.ac.uk

ABSTRACT

Bar colonization by vegetation and subsequent island formation is a key biogeomorphological process in fluvial landscape evolution. Here we investigate morphological and ecological evolution of river islands over timescales from single floods to decades, focussing on islands initiated by deposited trees that sprout to form vegetated patches.

On a braided reach of the high-energy Tagliamento River, Italy, we monitored 30 pioneer islands of 1-17 years age in comparison with unvegetated bar surfaces, open areas between
islands, and established islands surfaces. We integrated morphological, surface sediment
and vegetation properties of islands initiated by different flood events, combining evidence
from remotely-sensed and ground observations, flow and climate time series.

At a decadal time scale, pioneer islands aggrade rapidly to the elevation of the mean annual
flood, showing a steady increase in vegetation canopy height, fining of surface sediments
from predominantly gravel to silty-sand with a notable clay and organic fraction. The
standing vegetation included over 130 species, with the largest number on island surfaces of
intermediate elevation and flood disturbance. As islands age, standing vegetation becomes
comprised mainly of competitor species with transient seed banks and typical of woodland,
scrub, pasture and wetland habitats, whereas the winter seedbank is dominated on all
surfaces by ruderal species with persistent seedbanks, mainly associated with aquatic,
wetland, pasture, arable and wasteland habitats. At shorter timescales, the bio-
geomorphological trajectory of pioneer islands is initiated by large flood events that control
the elevation of deposited trees, and subsequent flows that control tree survival and
establishment. Island morphological evolution depends on the frequency-magnitude of
sediment and seed delivery and redistribution by flood and possibly wind events, whereas
island ability to retain sediments reflects the degree of vegetation establishment, which in the
short-term may vary with seasonal to annual moisture supply, substrate characteristics and
climatic growth conditions.

KEY WORDS

river islands, biogeomorphology, fluvial processes, riparian vegetation, wind

INTRODUCTION
Islands provide morphological and biological complexity to river environments (Ward et al., 2002b, Gurnell et al., 2005) and are an important element of river morphodynamics (Hupp and Osterkamp, 1996; Schnauder and Moggridge, 2009). Although the susceptibility of a river reach to island development depends primarily on physical setting and fluvial processes (e.g. Osterkamp, 1998, Osterkamp et al., 2001, Moretto et al., 2014, Perona et al., 2014, Baubiniené et al., 2015, Belletti et al., 2015), river islands develop within susceptible river reaches through interactions between vegetation and fluvial processes (Gurnell et al., 2001, 2012). Such interactions have been observed in the field (e.g. Corenblit et al., 2009, Wintenberger et al., 2015, Bywater-Reyes et al., 2017), through analysis of time sequences of aerial images (e.g. Bollati et al., 2015, Mardhiah et al., 2015, Corenblit et al., 2016) and in flume experiments (e.g. Bertoldi et al., 2015, Gran et al., 2015, Diehl et al., 2017).

Many different styles of island have been recognised and attributed to a variety of physical processes (e.g. Wyrick and Klingeman, 2011) but island development additionally reflects two broad types of interactions between vegetation and fluvial processes, either singly or in combination (Gurnell et al., 2001, 2012). ‘Building’ islands evolve as a result of the colonisation of mid-channel bars by vegetation and the further retention and stabilisation of sediment on the bars by vegetation. ‘Dissection’ islands are created by flows of water across pre-existing vegetated surfaces (e.g. floodplains, large islands), where the flow paths and the success of flows in dissecting the land surface depend to some degree on the distribution and type of vegetation that is present, and the degree to which root systems prevent or redirect the dissection and downcutting process. ‘Complex islands’ develop from some combination of these two processes.

In this paper we focus on ‘building’ islands, where vegetation colonisation and growth plays a pivotal role in the retention and stabilisation of materials that underpin the island’s aggrading morphology. Even in the lowest energy freshwater environments, retention and stabilisation of organic material, created by local vegetation under the influence of plant-groundwater-surface water interactions and related nutrient dynamics, underpins soil
formation and the topographic development of ‘tree islands’ (Wetzel, 2002). As flow energy increases, interactions between plants and physical processes of mineral sediment transfer and retention increasingly drive island development (Bertoldi et al., 2009). In addition, the range of plant species that are able to grow sufficiently rapidly to remain anchored and avoid uprooting or stripping by fluvial processes and to intercept, retain and stabilise organic and mineral sediments, reduces as flow energy increases. Thus, in relatively low energy river environments a range of both woody and non-woody plants can initiate island development by retaining and stabilising mainly finer sediments. However, as flow energy increases, plants that are able to engineer island development are predominantly woody. Furthermore, whereas seedlings of woody plants grow sufficiently rapidly to initiate island development on many rivers, in very high energy systems woody species that are able to propagate vegetatively become the main island engineers because of their ability to rapidly sprout and grow robust above- and below-ground biomass that can withstand strong shear stresses and deep burial during flood events (Gurnell, 2014).

Here we build on a conceptual model of island development proposed by Gurnell et al. (2001) that is applicable to high energy rivers of the northern temperate zone, where Salicaceae species dominate the riparian woodland. The model envisages three phases of building island development, from the deposition of entire uprooted trees and other living large wood (i.e. capable of resprouting) on bar surfaces during the falling limb of flood events, through an initial pioneer island phase of sprouting and sediment retention, to an established island phase as a result of the aggradation, enlargement and coalescence of pioneer islands. Since 2001, a number of refinements to the conceptual model have been introduced (Gurnell and Petts, 2002; Gurnell et al., 2012, 2016), and empirical evidence has been presented to support specific aspects of the model, including for example, island morphological (Bertoldi et al., 2011), sedimentological (Gurnell et al., 2008), soil (Mardhiah et al., 2014, Bätz et al., 2015), and vegetation development (Francis et al., 2008, Perona et al., 2014); living wood recruitment and dynamics (Bertoldi et al., 2013); early growth rates of
tree seedlings, cuttings and deposited trees (Francis et al., 2005, 2006, Francis and Gurnell, 2006, Francis, 2007; Moggridge and Gurnell, 2009) and interactions among developing subsurface tree root and shoot biomass and sediment retention (Holloway et al., 2017 a, b, c). In this paper we integrate empirical evidence of the processes and forms that accompany island evolution over decadal to event timescales, focusing on a single island-braided river reach of the Tagliamento River, Italy. Specifically, we consider:

(i) Trajectories of island topographic and vegetation canopy development based on the analysis of multi-temporal airborne Lidar data

(ii) Trajectories of vegetation succession and surface sediment development based on field sampling and measurements conducted on island and inter-island surfaces of different age

(iii) Short-term (seasonal, event) adjustments reflecting flow and surface sediment dynamics that may influence the longer-term trajectories identified in (i) and (ii)

METHODS

The research was conducted on a reach of the braided, gravel-bed Tagliamento River, Italy (Figure 1). The Tagliamento is one of the few European rivers that maintains largely intact morphological and ecological dynamism and complexity along much of its length, and is therefore considered a reference river system for the Alps and a model system for large rivers (Tockner et al., 2003). The river runs 172 km from source to mouth and its climate varies from alpine to mediterranean. Most importantly for this research, it maintains river islands along several reaches, which have been the focus of a range of hydrogeomorphological and ecological investigations over the last two decades (see Gurnell, 2016). The island-braided reach focused on here (46°12' N, 12°59' E) is in the prealpine section (140 m a.s.l.) and has a wet mediterranean climate with a mean annual precipitation of approximately 2000 mm. Peak river flows are in spring (snowmelt) and autumn (rainfall).
The water table at the study site showed subdued variation through the year as a result of groundwater upwelling induced by local narrowing of the river valley towards a gorge section approximately 2 km downstream.

Information was assembled from airborne Lidar surveys, river stage records, field campaigns and the laboratory analysis of field samples to investigate the morphological, surface sediment and vegetation evolutionary characteristics of islands within the study area. The timing of the Lidar surveys, tree deposition events that initiated the studied pioneer islands, and field measurement campaigns are plotted in relation to the January 2000 to February 2017 time series of daily river stage (corrected to detrended elevations within the study reach, see below for correction method) in Figure 2.

**Lidar data, river stage and climate station records**

Three airborne Lidar surveys were available for analysis, captured in May 2005, August 2010 and October 2013. The Lidar surveys covered the study reach and had a spatial resolution ranging from 1 (2005 survey) to approximately 10 points/m² (2013 survey). These were analysed to obtain tree canopy height and detrended surface elevations for all field sampling locations on surfaces of different age and type (see the following subsection on ‘Field sampling and measurements’).

The free software FUSION, developed by the U.S. Department of Agriculture, Forest Service, Remote Sensing Applications Center (available at http://www.fs.fed.us/eng/rsac/) was employed to filter the Lidar point cloud differentiating between ground points and vegetation points. From this information we obtained a Digital Elevation Model (DEM) and a Canopy Surface Model (CSM), with a spatial resolution of 2 m for 2005 and 1 m for 2010 and 2013 (see Bertoldi et al., 2011 for further details). River bed and vegetation canopy elevations were extracted from these two raster data sets within circular areas of 5 m radius centred on the 2016/2017 field sampling locations. Since there was considerable flood
disturbance of lower areas of the river bed between October 2013, when the most recent
Lidar data were captured, and 2014, when the trees initiating the youngest studied pioneer
islands were deposited, analysis of the Lidar data was confined to sampling points on
established islands (probably initiated in the mid to late 1970s, hereafter conservatively
labelled 1980), pioneer islands initiated in 2000 and 2004, and surfaces between the 2000
and 2004 islands.

The extracted elevation data was detrended to remove the impact of the down-valley slope
and thus highlight the relative cross-sectional river bed elevation of the sampling locations
and sites. Detrending was achieved by computing a moving average of the 2005 DEM,
based on an 800 m square window (800 m approximates the typical width of the active river
corridor). Within each 800 m square window, areas outside of the active corridor were
excluded when calculating the average bed elevation, which was then subtracted from all
three DEMs to allow for a direct comparison of the temporal evolution of the different
surfaces.

In order to explore the degree to which detrended surface elevation and vegetation canopy
height varied across the different sampled surfaces, through time, and in relation to
interactions between surfaces and time, generalised linear models were estimated to explore
the dependence of vegetation canopy height and surface elevation on sampled surfaces,
year of Lidar observation, and interactions between surface and year. The statistical
significance of differences between particular surfaces, years and surface-year interactions
were explored using the Bonferroni method (P<0.05).

River stage records from the Villuzza gauging station, located approximately 2 km
downstream from the study reach, provided information on flow events and sequences to aid
interpretation of the morphological, sedimentary and vegetation data sets that were
collected. River stage at Villuzza was linked to the detrended bed surface elevation of the
study reach using oblique photographs captured with a temporal resolution of one hour by
applying the method described by Bertoldi et al. (2009) and further developed by Welber et
al. (2012). Inundation maps at different flow stage were compared to the 2010 and 2013 DEMs to obtain a relationship that transformed the river stage measured at Villuzza into the detrended DEM elevation coordinates. This allowed the frequency of inundation of the sampled locations and sites, based on 2000-2017 daily maximum stage records, to be estimated as well as their potential inundation between the two sampling campaigns in 2016 and 2017.

Air temperature, solar radiant energy exposure, precipitation and wind speed data from a climatological station at Osoppo, about 7 km upstream (North-East) of the study reach, was used to explore conditions relevant to the interpretation of field data. In particular, air temperature data were used to estimate accumulated Growing Degree Days (GDD) that could indicate likely vegetation development at the time of field surveys. GDD was estimated as follows:

\[
\text{accumulated GDD} = \sum_{i} \left( \frac{T_{\text{max}} + T_{\text{min}}}{2} - T_{\text{base}} \right)
\]

Where \(T_{\text{max}}\) and \(T_{\text{min}}\) are the maximum and minimum temperature on each day, \(T_{\text{base}}\) is 10°C, 1 is 1\(^{st}\) January and \(n\) is the Julian day for which the estimate is required. This was complemented by analysis of accumulated solar radiant energy exposure.

Wind speed and precipitation data were combined with river stage information from the Viluzza gauge to explore climate conditions between field surveys.

**Field sampling and measurements**

Several types of sampling and measurement were undertaken in the field.

Surface sediments were sampled from 14\(^{th}\) to 17\(^{th}\) June 2016 and 22\(^{nd}\) to 23\(^{rd}\) February 2017 to investigate their calibre, organic content and viable seed content. Following previous detailed analysis of historical air photographs to confirm timing of tree deposition / island initiation and estimation of contemporary tree ages using dendrochronology (Mardhiah et al.,}
209 2015), samples were taken from surfaces of known age representing established islands (EI)
210 initiated in the mid to late 1970s (1980EI); pioneer islands (PI) initiated during floods in late
212 pioneer islands (2000btwn, 2004btwn) and across the unvegetated surface of gravel bars
214 tree (2000PI, 2004PI) or a central point along the deposited tree (2014PI); the largest
215 (oldest) trees on established islands (1980EI); locations close to the sampled pioneer islands
216 but not on island surfaces (2000btwn, 2004btwn) and randomly located locations on
217 unvegetated bar surfaces (unveg). In each case a cylindrical, 6 cm diameter sediment sub-
218 sample was taken to a depth of 5 cm at the central location and at approximately 5m
219 upstream, downstream and to either side of this central location. Where sampled pioneer
220 islands were less than 10 m in either length or width, sub-samples were taken as far as
221 possible from the centre up to a distance of 5 m but within the morphological limits of the
222 island. A single aggregate sample was generated for each sampling location by combining
223 these five subsamples. Aggregate samples were obtained from ten different sampling
224 locations (Figure 1) for each of the surfaces of different age (1980EI, 2000PI, 2004PI,
225 2014PI, 2000btwn, 2004btwn, unveg). This yielded a total of 70 aggregate samples for June
226 2016 and 69 for February 2017 (one 2014 pioneer island was removed by an intervening
227 flood and so could not be sampled). Although islands exhibit high vertical heterogeneity and
228 distinct layering of sediments as a legacy of past disturbance events, previous investigations
229 of sediment profiles to depths of over 1.5 m below the surface of established islands have
230 revealed a weak upward fining of sediments, typically with a distinct sand and finer layer at
231 the surface (for example, see profiles illustrated in Holloway et al., 2017b). In the present
232 analysis, we focused on the top 5cm of sediment as this is not only indicative of the most
233 recent sediment deposition but, as a consequence, it is most likely to contain viable
234 propagules, recently deposited through local seed fall, anemochory or hydrochory. It is also
235 the most relevant to plant germination. Furthermore, seed bank studies are typically
236 conducted on samples taken to a depth of 5 cm (Thompson et al., 1997).
In addition to sampling surface sediments, in June 2016 the height of the 2000PI and 2004PI central trees was also measured using a clinometer, and a vegetation survey was conducted at 5 of the sampling locations (area approximately 10m x 10m) on each of the island surfaces of different age (1980EI, 2000PI, 2004PI, 2014PI). Information was also available from a vegetation survey conducted in July 2011 using the same methodology. This survey focussed on five 2000, five 2004 and five 2010 pioneer islands. The last were almost 1 year old at the time of the 2011 survey and so provide a comparison with the 2014 pioneer islands that were approximately 1.5 years old when surveyed in 2016.

Surface sediment analysis

Following field sampling, all the aggregate surface sediment samples were air dried and passed through a 4 mm sieve at the field station to ensure retention of all viable seeds. The weight of sediment and coarse organic material in the >4 mm fraction were separately weighed at the field station and an approximate 300 g subsample of the <4 mm fraction was transferred to a UK laboratory for organic matter and particle size analysis (described in this section) and investigation of the soil seed bank (described in the following section).

In the laboratory, organic content of the <4 mm fraction of all 139 samples was determined by loss on ignition, and the mineral particle size distribution was determined at a resolution of 1 φ from -2 φ (4 mm) to -12 φ by sieving through 2 mm (-1 φ) and 1 mm (0 φ) sieves and then passing a subsample of the <1 mm fraction through a laser sizer to identify the particle size distribution below 1 mm (0 φ).

Multivariate analyses were used to investigate broad patterns in the values of six summary properties of the surface sediments: %organic (of the total sample), D50 (φ), %gravel, %sand, %silt, %clay (of the total mineral fraction). The six variable data set was analysed using Agglomerative Hierarchical Cluster Analysis (AHC) with Euclidean distance as the distance measure and Ward’s clustering algorithm. The number of clusters that most
effectively summarised variations in the samples was selected using the AHC agglomeration
schedule plot coupled with an analysis of the statistical significance of differences among the
six surface sediment properties between the clusters. The statistical significance of
differences between clusters was assessed using Kruskal Wallis tests followed by multiple
pairwise comparisons using Dunn’s procedure with Bonferroni correction of the significance
level. This non-parametric test was selected because most of the variables were measured
on a percentage scale, and thus values were confined to the range 0 to 100.

Principal Components Analysis (PCA) was also applied to the six surface sediment property
data set to assess whether any broad gradients were present in the data that could support
interpretation of contrasts between the sampled surfaces of different age and type. Because
most of the surface sediment properties were expressed as percentages, the PCA was
performed on a (non-parametric) rank correlation matrix. In order to illustrate contrasts
between the surface sediment classes identified by AHC, samples were coded by sediment
cluster or class on a scatter plot of each sample’s score on the first two PCs.

An average distribution for each surface age and sampling date (i.e. averages of ten particle
size distributions) was calculated for particle size distributions for the <1mm (0 ϕ) mineral
fraction (i.e. coarse sand and finer), which was entirely analysed by laser sizer. Overlays of
the average distributions were used to explore changes in the composition of the mineral
sediment in this coarse sand and finer fraction between sampling dates on the surfaces of
different age. The differences between groups of particle size distributions drawn from
different surfaces on two sampling dates (June 2016, February 2017) were investigated by
estimating generalised linear models for each of the ten, fifty and ninety percentiles (D10,
D50, D90) of the particle size distributions, using sampling year (2016, 2017), surface
year and surface as the explanatory variables. The percentile values were estimated using
Gradistat software (Blott and Pye, 2001) and are expressed in ϕ units. The statistical
significance of differences between groups was established using the Bonferroni method (P<0.05).

Standing vegetation and soil seed bank analysis

The viable seed bank contained in the February 2017 surface sediment samples was quantified using germination trials. By gathering surface sediments in February, only the more persistent seed bank was sampled, since few species produce seeds during winter. Subsamples of 60 gms weight were extracted from the <4 mm fraction of the aggregated surface sediment samples from each sampling location and were refrigerated (circa 4°C) on arrival at the laboratory. These were stored until June 2017, when a 10 week germination trial was conducted in outdoor poly-tunnels. No artificial lighting or heating was used in the tunnels. The sediment subsamples were sprinkled onto 3 cm deep sterile soil (John Innes #2) in 10 cm x 20 cm seed trays. The seed trays were watered regularly to maintain the soil at field capacity, and the trays were rearranged in the poly-tunnels at the end of each week to randomise germination conditions. As seeds germinated, the seedlings were identified to species and then removed from the trays. In some cases the seedlings were transferred to individual pots and grown on to support species identification. From these data, the number of viable seeds per m² and seed species composition were estimated for each sample. In order to compare with other living components of organic material in the sampled sediments, information on seed abundance (seeds per m²) in the February 2017 seedbank was compared with information on root and hyphal length collected across islands of different age (1980, 2000, 2004, 2010) and unvegetated bar surfaces (unveg) during May 2012 (for analytical methods see Mardhiah et al., 2014).

The standing vegetation was also surveyed on two occasions. Between 18 and 20 June 2016, the standing vegetation was recorded on five pioneer island and established island surfaces of different age (2014PI, 2004PI, 2000PI, 1980EI). A walk over survey was
conduct within the approximate 10m by 10m area from which surface sediment samples were taken and the presence of plant species was recorded within a search period of up to 1 hour. A survey of the standing vegetation was also conducted between 22 and 25 July 2011 using exactly the same methods as in June 2016, although only pioneer islands were surveyed. Five randomly selected pioneer islands dating from each of 2000, 2004 and 2010 (close to 1 year old at the time of survey) were surveyed.

Using information from Hodgson et al. (1995), the seed bank type (i.e. transient, short-term persistent, long-term persistent), most common terminal habitat, and functional type (Grime et al., 2007) were identified for as many of the species recorded in the standing vegetation and seed bank as was possible. For functional type, a score between 0 and 1 was assigned to C (competitor), S (stress-tolerator) and R (ruderal) components of the CSR functional type for each species (Hunt et al., 2004) to allow quantitative comparisons between sampling locations and between the species found in the two standing vegetation surveys and the seedbank germination trial. These properties of the standing vegetation and seedbank were then displayed using bar graphs to explore any apparent changes in the proportions of functional types present according to surface age. Similarities in the species composition of the standing vegetation and viable seed bank were assessed using Agglomerative Hierarchical Cluster analysis with the Jaccard coefficient as the similarity measure and clustering determined using the unweighted pair group average.

All statistical analyses presented in this paper were conducted using Minitab 18 or XLSTAT 2017.

RESULTS

Surface elevations and inundation frequency.

A generalised linear model revealed statistically significant variations in detrended river bed elevation across different surfaces and through the time sequence of Lidar surveys, but
there were no significant interactions between surfaces and time (Table 1). Bed elevations were significantly higher in 2013 and 2010 in comparison with 2005, and the sampling sites on the 1980 established island surfaces were significantly higher than the pioneer island and between-island sampling sites initiated in 2000, which were in turn significantly higher than surfaces initiated in 2004. However, there was high variance in the elevation of the pioneer island and between island surfaces initiated in 2000 and 2004, and thus there was no statistically significant difference in the elevation of the pioneer island and between island surfaces initiated in either 2000 or in 2004.

The inter-quartile ranges in the detrended elevation of sampling locations on the 1980, 2000 and 2004 surfaces are illustrated in Figure 3 in relation to the water level duration curve (estimated from 2000-2017 daily maximum stage records at Viluzza). The interquartile ranges indicate that at the time of the 2005 Lidar survey, the recently deposited 2004PI were inundated between approximately 9 and 40 days each year, whereas the 2000PI were inundated between 0.8 and 3 days per year and the 1980EI were sufficiently elevated that they were not inundated by the 2 year return period flood. These large differences in inundation frequency explain why the interquartile ranges indicate a clear increase in detrended surface elevation of the 2004PI and 2004btwn sampling locations through time. The upper quartile of these elevations reaches the lower quartile of the 2000PI and 2000btwn sampling locations by 2013. The maximum water stage reached between sediment sampling campaigns in June 2016 and February 2017 is also indicated on Figure 3, showing that most of the 2004 sampling locations were inundated during this period, whereas all of the 1980EI and most of the 2000PI and 2000btwn sampling locations were not inundated.

Surface sediment composition
AHC applied to six surface sediment properties (D50(\(\phi\)), %organic, %gravel, %sand, %silt, %clay) yielded six significantly different clusters, which characterised distinct sediment classes within the 139 aggregate samples that were analysed. The number of samples assigned to each class and the centroid values of each surface sediment property within the six classes are presented in Table 2 and the degree to which each of the six properties displayed by sediment samples assigned to each class displayed significant differences are also summarised in Table 2.

PCA identified two major gradients or PCs that together explained 93% of the variance in the six variable data set. Focussing on high (>0.7 and <0.7) PC loadings (Table 3), PC1 describes a gradient of decreasing %gravel (high negative loading) and increasing %silt, %clay, %organic and median particle size (D50 in \(\phi\) units indicating sediment fining) (high positive loadings), whereas PC2 describes an independent gradient of increasing %sand.

The AHC and PCA results are combined in Figure 4, where they can be compared with the surface type, age and survey year relevant to each sample, displayed on a scatter plot of the sample scores on the first and second PCs identified in the PCA. These scatter plots indicate that samples drawn from unvegetated bar surfaces (unveg), between pioneer islands (2000btwn, 2004btwn) and from the youngest pioneer islands (2014PI) (Figure 4 (i)) are predominantly associated with gravel, gravel-sand and sand-gravel sediments (classes A, B, C, Figure 4 (iv)). The older pioneer (2004PI, 2000PI) and established (1980EI) islands show a range of surface sediment sizes from predominantly sand, through sand with some silt, to sand-silt sediments, with a progressive increase in the D50 (in \(\phi\) units, indicating sediment fining) and organic content (classes D,E,F, Figure 4 (iii)) with increasing surface age (Figure 4 (v)). There is also some evidence of a change in surface sediment characteristics between summer 2016 and late winter 2017 (Figure 4 (ii)), particularly a shift from sand towards silt and clay (Figure 4 (iii)) in the area on the right of the plot, where scores on PC1 exceed 0 (Figure 4 (ii)).
Focussing on the <1mm (>0 ϕ, coarse sand and finer) sediment fraction (Figure 5), which is
the size fraction analysed entirely by laser sizer, the average particle size distribution for all
surfaces appears to fine between June 2016 samples and February 2017 apart from those
extracted from established island (1980EI) and unvegetated surfaces (Figure 5, compare A
and C with B and D). The most pronounced changes are observed for the 2004PI, 2014PI
and 2004btwn locations. The change for 2014PI is particularly noticeable, moving from a
distribution that is very similar to the unvegetated (unveg) surfaces in 2016 to a distribution
that is approaching that of the vegetated surfaces (2004PI, 2000PI, 1980EI) in 2017,
indicating a fast evolution of these finer sediments on pioneer islands in their first 1 to 2
years.

This apparent fining trend in the < 1mm fraction is supported by box plots and generalised
linear models for the D10, D50 and D90 percentiles (in ϕ units) of the 10 individual particle
size distributions within each of the surface and sampling time groups (Figure 5E, F and G).
The generalised linear model for the coarsest percentile (D10, Table 4), explains 66% of the
variance, with a statistically significant overall fining of sediment between years, a significant
decrease in the D10 particle size between the older island surfaces (1980EI, 2000PI,
2004PI), the youngest PI and oldest between island surfaces (2014PI, 2000btwn), and the
youngest between island and unvegetated bar surfaces (2004btwn, gravel). There were no
statistically significant interactions between surfaces and year. This is supported by the box
plots (Figure 5E), which show little change between years apart from a slight hint of fining on
the youngest island (2014PI) surfaces. The results from this analysis should be treated with
a little caution because some estimated D10 values for the coarsest samples (mainly from
2004btwn and unveg surfaces) fall between 0 and -1 ϕ (i.e. slightly larger than the less than
1 mm (0 ϕ) range of the analysed data). This is an artefact of the very large percentage of
particles in the 0 to 1 ϕ fraction in these relatively coarse samples, which have highly skewed
frequency distributions. The model for D50 particle size is similar to that for D10 (Table 4,
Figure 5F), explaining 62% of the variance, and revealing the same statistically significant
patterns in fining between years and surfaces with no statistically significant interactions between years and surfaces. However, the finest percentile (D90) reveals a more complex fining pattern (Figure 5G, Table 4). The generalised linear model explains 57% in the variance of D90. Once again there is a statistically significant overall fining of surface sediment between years. The older island surfaces (1980EI, 2000PI, 2004PI) are finer than the between island surfaces (2000btwn, 2004btwn), which are finer than the open, unvegetated surfaces (unveg). In addition, the youngest island surfaces (2014PI) are finer than the unvegetated bar surfaces (unveg). There are also some significant year-surface interactions within the D90 data. The older island surfaces in both years (1980EI, 2000PI, 2004PI) and the youngest island and between island surfaces (2014PI, 2000btwn, 2004btwn) in 2017 are finer than the between island surfaces (2000btwn, 2004btwn) in 2016 and the unvegetated surfaces (unveg) in both years. These results illustrate a stronger fining of between island and younger island (2014PI, 2000btwn, 2004btwn) surfaces than other surfaces between the two survey years.

A final investigated property of the surface sediments was the living organic material that they contain. Some living components are illustrated in Figure 6, including viable seeds per m² estimated from the February 2017 surface sediment samples (Figure 6B), and the fungal hyphae (Figure 6C) and root content (Figure 6D) estimated from samples extracted from different surfaces during May 2012 by Mardhiah et al. (2014). Each of the three graphs in Figures 6 B, C and D represents a snap shot of properties that vary greatly through time. However, it is interesting to note that while roots and hyphae, which are largely developed in situ, show a steady increase with surface age, seeds, which may be deposited locally but are also subject to transport and deposition by various agents (e.g. water, wind), show a more variable pattern with greatest abundance on the 2004PI surfaces at the time of sampling, whereas unvegetated surfaces show the lowest abundance.

Vegetation
Vegetation canopy height estimates from the three Lidar surveys (2005, 2010, 2013) and field clinometer measurements (2016) are shown in Figure 6A. Clinometer measurements were only made at the 2004PI and 2000PI sampling locations, where both the top of the canopy and the underlying ground surface could be seen clearly from a single measurement point and thus accurately measured. The two box plots for these 2016 field measurements indicate a realistic increase from the earlier Lidar estimates for the same surfaces and sampling locations, suggesting that the Lidar estimates of canopy height for the other three dates are quite accurate. Overall the island surface data (1980EI, 2000PI, 2004PI) presented in Figure 6A define a growth curve for the *P. nigra* dominated woodland within the reach. This indicates rapid vertical growth of approximately 1m each year for at least the first 15 years, after which vertical growth reduces as this species approaches maturity. The data also illustrate the development of some vegetation cover between pioneer islands.

A generalised linear model for vegetation canopy height reveals statistically significant (P<0.05) differences among the surfaces, through the time sequence of surveys, and also significant interactions between surfaces and time (Table 1). Canopy height increased significantly from 2005 to 2010 and then to 2013. Furthermore, the canopy was higher at 1980EI locations than at 2000PI locations, which was in turn higher than at 2004PI locations, and again higher than at 2000btwn and 2004btwn locations. Significant interactions illustrate how in 2005 all 2000PI and 2004PI surfaces had a low vegetation canopy that was not significantly different from the 2000btwn and 2004btwn locations. However, in later surveys, the canopy progressively increased in height across the 2000PI and 2004PI surfaces, so that the canopy on 2000PI surfaces in 2013 was significantly higher than that on 2000PI surfaces in 2010 and the canopy on 2004PI surfaces in 2013, and these in turn were higher than the canopy on 2004PI surfaces in 2010. The 1980EI surfaces supported the highest vegetation canopy at all dates.

The composition of the vegetation was explored in July 2011 and June 2016 through walk-over surveys of 5 pioneer islands of three different ages. Pioneers islands initiated in 2000
and 2004 were explored on both dates as well as newly formed pioneer islands (2010PI in the 2011 survey and 2014PI in the 2016 survey). In addition surveys at five of the 1980EI sampling locations were explored in 2016. Viable seed species were also identified for all 2017 sampled surfaces (1980EI, 2000PI, 2004PI, 2014PI, 2000btwn, 2004btwn, un veg).

In total, 138 plant species were identified across the three surveys. In addition to the earlier survey date, there was a colder spring in 2016 than in 2011. The accumulated growing degree days (GDD) to 18 June 2016, when the vegetation survey commenced, was 470 in comparison with 632 to the same date in 2011, and the accumulated GDD to 22 July 2011, when the vegetation survey commenced in 2011, was 1040. The accumulated solar radiant energy exposure from 1st January to 18th June 2016 was 1752 MJ/m² and from 1st January to 18th June 2011 was 2339 MJ/m² (about 33% more than in 2016 for the same time period). The accumulated solar radiant energy from 1st January to 22nd July 2011 was 3104 MJ/m².

These contrasts in accumulated GDD and solar energy receipt probably explain differences in the standing vegetation. Few species were in flower and many species had probably not emerged sufficiently to be recorded during the June 2016 vegetation survey, whereas vegetation development was much more advanced during the 2011 survey. While 105 species were recorded in the standing vegetation in July 2011, only 76 were recorded in June 2016, and only 30 were recorded in the February 2017 seed bank. Of the 138 recorded species, seven (less than 5%) were alien (*Amorpha fruticose, Aster novi-belgii, Buddleja davidii, Conyza Canadensis, Datura stramonium, Juncus tenuis, Robinia pseudoacacia*). Of the 30 species identified in the seedbank only two (7%) were alien: *Buddleja davidii* and *Juncus tenuis*. The number of viable seeds in the winter seedbank should also be considered in the light of the stark contrasts in the longevity of the seedbanks associated with the standing vegetation observed across the different types and ages of sampled surfaces described below.

Agglomerative Hierarchical Cluster Analysis was used to explore the similarity in species composition of the standing vegetation (2011, 2016) and the seed bank (2017) (Figure 7).
The seed bank composition showed very little similarity to the standing vegetation. There was also a contrast in species composition displayed by the two standing vegetation surveys. The species composition of pioneer islands surveyed in 2011 showed reasonable similarity and clustered in turn with the 2000 and 2014 pioneer islands surveyed in June 2016. However, the vegetation species composition of 2004 pioneer islands surveyed in 2016 was most similar to the 1980 established islands, whereas that of the 2000 pioneer islands surveyed in 2016 was most similar to the 2014 pioneer islands. Furthermore, vegetation composition of the latter was more similar to pioneer islands surveyed in 2011 than to the 2016 vegetation of the 2004PI and 1980EI surfaces. This illustrates some notable differences in the rate of development of vegetation on pioneer islands of different date.

Broad characteristics of the identified species are summarised in Figure 8. Far fewer species were found in the seed bank than in the standing vegetation (Figure 8A). Information on 67% (92) of these species was extracted from Hodgson et al. (1995) and Grime et al. (2007). In a few these cases, where the specific species was not included, it was possible to extract plant strategies and characteristics based on closely related species in the same genus. The number of species according to data source (seed bank, standing vegetation), sampling date and surface type for which characteristics were extracted from Hodgson et al. (1995) is illustrated in Figure 8A (labelled ‘species analysed’). Three characteristics of the analysed species - functional type, seed bank type, typical terminal habitat type - are summarised in Figures 8B, C and D, respectively, across the seed bank and standing vegetation data sets for surfaces of different age.

The February 2017 seed bank was dominated by species whose primary strategy was ruderal, whereas predominantly competitor species were present in the standing vegetation (Figure 8B). Furthermore, the competitor strategy was stronger in species observed on the 2004 and 2000 pioneer islands and 1980 established islands than on the early stage pioneer islands (2010 and 2014). Seed bank persistence also varied across the species identified in the seed bank and standing vegetation (Figure 8C), with the seed bank, particularly on
unvegetated bar and between-pioneer island surfaces, being dominated by species associated with a long-term persistent seed bank (i.e. seeds remaining viable for at least five years), whereas the standing vegetation on pioneer and established island surfaces shows an increasing proportion of species associated with a transient seed bank (i.e. seeds that rarely remain viable for more than a year) as the age of the surface increases. The 1980EI surfaces are dominated by species with a transient seed bank (62% species) and a very small proportion (15%) are associated with a long term persistent seed bank.

There are also strong contrasts in the commonest terminal habitat with which the species are associated (Figure 8D). In Figure 8D, the terminal habitats listed in Hodgson et al. (1995) have been aggregated into broad groups related to moisture, vegetation cover and type and degree of natural or human disturbance. The February 2017 seed bank contained a number of species associated with water habitats that were not observed in the standing vegetation, almost no species associated with woodland, none associated with scrub, but species associated with pasture and meadow habitats were present. In contrast, the standing vegetation displayed species whose terminal habitats included pasture and meadow, scrub and woodland, and the proportion of species associated with these terminal habitats increased with surface age. At the same time, although no species associated with water habitats were observed in the standing vegetation, wetland species were present in a declining proportion with surface age and three river bank species were found only in the standing vegetation of pioneer islands. Species associated with bed rock and scree habitats were present in the standing vegetation and seed bank of all investigated surfaces apart from the seedbank samples drawn from unvegetated and between pioneer island surfaces. However, species associated with wasteland habitats were mainly confined to the standing vegetation.

DISCUSSION
The results presented in this paper support discussion of the evolution of islands over years to decades and also the influential processes that occur over days to months. These themes are discussed below in two subsections, and are followed by a final subsection which includes some concluding remarks and reference to management applications.

Evolution of islands over years to decades

Analysis of aerial images (Mardhiah et al., 2015) and field observations confirm that established and pioneer islands that persisted and developed up until the last field campaign in 2017 were initiated by deposition of uprooted trees during flood events that occurred in the mid to late 1970s and during 2000 and 2004 (the last two characterised by a recurrence interval of >10 years and 3 years, respectively). Therefore, pioneer island establishment is not a frequent process. Specific conditions are needed that occur occasionally when compared with the starting processes of vegetation erosion and large wood deposition, which have been observed to occur during low magnitude floods with a recurrence interval in the range 1 to 2.5 years (Bertoldi et al., 2013; Surian et al., 2015). Flood history appears to be more relevant than peak magnitude in island development, as also highlighted by Belletti et al. (2014) in their regional scale study of 12 braided rivers. A combination of morphological reworking, the creation of appropriate surfaces, vegetated bank erosion and deposition of the uprooted trees, followed by a few years of lower flow are all necessary. For example, evidence from airborne Lidar surveys shows a gradual but clear aggradation of the 2004PI surfaces over an 8 year period. Their median detrended elevation increased from -0.285 m in 2005 to +0.168 m in 2010 to +0.176 m in 2013 (average aggradation of approximately 0.057 m per year). These 2004 pioneer islands were initiated at a very low elevation, compared to that of other uprooted and deposited trees observed in the same reach. Bertoldi et al. (2013) reported trees deposited in the range 0 to 0.5 m during a flood in 2009, and those did not survive subsequent floods. Furthermore, although the 2014 deposited trees could not be located on the 2013 Lidar, it is very likely that they were
deposited at an elevation of approximately 0.1-0.3 m, comparable to that of the 2004 pioneer islands almost 10 years after deposition. A similar wide range of deposited tree elevation was reported also by Räpple et al., 2017 (when transformed from elevation above low flow to elevation above the mean). This reinforces the crucial role played by flood history. The survival of the 2004 pioneer islands was possible only because of the occurrence of 3 particularly dry years following their deposition, enabling deposited trees to anchor themselves and grow before being affected by significant flood disturbance.

The evidence for aggradation of the older and higher 2000PI and 1980EI surfaces over this period is equivocal, suggesting a rapid slowing in aggradation once island surfaces have developed above the level of relatively frequent inundation (e.g. elevations that are reached for less than one day per year, Figure 3).

The islands developed around deposited uprooted trees and aggraded as new trees sprouted from them (e.g. Figure 1, 2002 image shows sprouting trees deposited in 2000). In nearly all cases, the deposited trees that initiate pioneer islands in the study reach are black poplar (*Populus nigra*), a facultative phreatophyte capable of rapid root growth in response to different water and sediment conditions (Holloway et al., 2017a, b, c), and the Lidar data and field measurements show that deposited trees of this species can regenerate to produce a canopy that grows rapidly, particularly in the first 15 years following deposition (Figure 6A).

The median canopy height increased from 0.24 to 6.85 m (6.61 m growth) on the 2004PI surfaces, from 1.64 to 9.76 m (8.72 m growth) on the 2000PI surfaces and from 22.79 to 25.04 m (2.25 m growth) on the 1980EI surfaces between 2005 and 2013. These data suggest that after the first couple of years following deposition, an annual growth increment of over 1 m per year above the aggrading island surface is achieved in the study reach over at least a 15 year period. Since the growth develops from a deposited tree, which then becomes buried, the actual annual growth rate from the elevation at which the tree was deposited is slightly greater than this in these early years.
As islands aggrade, they also extend laterally through aggradation and coalescence. This lateral aggradation can be clearly seen in the vegetated area surrounding the studied 2000 and 2004 pioneer islands in Figure 1 (compare the 2002 and 2015 images at the sampling locations), and is supported by increases in vegetation canopy height and emergence of a vegetation canopy between pioneer islands (Figure 6A). The annual growth rate of trees on the 2000 and 2004 pioneer islands is quite constant when measured on a time scale of 3 to 5 years, with no apparent marked changes between particular years (Figure 6A). The time scale is probably long enough to filter out the impact of annual changes in temperature and precipitation, masking the controls highlighted by Räpple et al., 2017. More importantly, once the trees have survived initial deposition and early establishment, which is affected by access to groundwater and thus river stage (e.g. Francis, 2007), there seems to be a negligible impact of local bed elevation on their rate of growth. This comparable growth rate regardless of elevation indicates high water availability in the study reach, which is mainly characterised by groundwater upwelling (Doering et al., 2007). On other reaches of the Tagliamento, such a constant rate of growth may not occur, since there are notable differences between reaches (Gurnell, 2016) that highlight sensitivity to changes in moisture availability, and such sensitivity to relative elevation with respect to groundwater may be an important factor in island development across other river environments.

As sediments accumulate around the growing *P. nigra* trees, their properties change (Figure 4). While unvegetated bar surfaces are characterised by gravel deposits, higher surfaces show increasingly fine deposits. Well-vegetated island surfaces (1980EI, 2000PI and 2004PI) show predominantly sandy surface sediments containing varying amounts of silt, clay and organic material, whereas sparsely-vegetated surfaces of the youngest pioneer islands (2014PI) and areas between the older pioneer islands (2000btwn, 2004btwn) show coarser gravel-sand mixtures (Figure 4). Thus sediments fine with increasing elevation and vegetation cover, presumably because finer sediments on sparsely-vegetated elevated surfaces between pioneer islands are subject to flow funnelling and higher shear stresses.
during major inundating flood events that may mobilise finer sediments. The role of fine
sediments is relevant for island development, but not crucial for island initiation. Deposited
trees are able to trap fine sediments soon after they sprout and grow branches and leaves.
For example, after less than 2 years and a few moderate floods, the grain size distribution of
the 2014PI surfaces show a clear fining. The subsequent growth of shrubs and then herbs
and grasses forms a vegetated surface that is increasingly efficient at trapping fine
sediments and organic matter as islands age.

The number of plant species and the vegetation composition of islands also changes with
increasing age (Figure 8). Focussing on the vegetation survey conducted in 2011 and
following a warm spring, the number of species in the standing vegetation increases steadily
from 1 year old (2010PI) through seven year old (2004PI) to 11 year old (2000PI) islands as
new species progressively colonise the developing island surfaces (Figure 8A). The 2016
vegetation survey, following a cool spring, recorded fewer species than the 2011 survey,
with little difference in the number of species on two year (2014PI) and 12 year (2004PI)
pioneer islands. The largest number of species were observed on 16 year old pioneer
islands (2000PI), with established islands (1980EI) showing less species than all of the
pioneer islands (Figure 8A). This suggests that as islands aggrade, new species appear until
the tree canopy closes and the trees and shrubs out-compete many other species, following
typical seral trajectories wherein species are excluded by dominant competitors and diversity
peaks in the mid-seral stages; though this trend is also likely to be an expression of the
intermediate disturbance hypothesis (Connell, 1978; Tabacchi et al., 1998; Bendix and
Hupp, 2000) whereby the largest number of species are supported on surfaces subject to an
intermediate level of flood disturbance. However, the reduction in species present on
established island surfaces is likely to be counteracted by species colonising areas of wood
and sediment deposition, sprouting and aggradation at and near island edges that create
new local island-margin patches, particularly at the sheltered downstream island tail, that
may emulate the vegetation development processes observed on pioneer islands.
The supposition concerning canopy closure and competition is also supported by the average C, S and R scores of the species that are present. With increasing surface age, the vegetation becomes increasingly dominated by competitor species, whereas the youngest pioneer islands show a balance of competitor, stress-tolerator and ruderal species (Figure 8B). Furthermore, the proportion of species associated with wetland, arable, wasteland and bedrock terminal habitats decreases and the proportion with woodland and scrub terminal habitats increases with surface age (Figure 8D), as a more stable ‘climax’ riparian woodland emerges. The change in vegetation cover, height and composition with increasing island age is accompanied by an increase in the organic content, roots and fungal hyphae as the fining surface sediments start to develop into soils with increasing island age (Figure 6).

These observations support the island development model proposed by Gurnell et al. (2001) and provide considerable detail on the functioning of that model over annual to decadal timescale.

Influential processes over days to months

Large flood events are crucial to the island model, and so it is unsurprising that the largest flood in the period 2000 to 2017 (on 5th November 2000, Figure 2) was responsible for initiating numerous, widely distributed pioneer islands in the study reach. The flood event in 2004 (on 31st October, Figure 2) was more localised than the 2000 event with trees released by erosion of the floodplain around a tributary being deposited across a relatively small area of the river bed (Francis et al., 2008). However, the resulting pioneer islands have grown rapidly to the present, despite the occurrence of a larger flood in 2012 (on 12th November, Figure 2). This survival can probably be attributed to a four year period without significant floods following the 2004 event, which allowed these 2004 pioneer islands to establish and aggrade sufficiently to resist erosion. The occurrence of the large flood in 2012 may also explain why trees deposited by smaller flood peaks on 30th October 2008, 25th December
2009 and 1\textsuperscript{st} November 2010 (Figure 2) have not developed into longer-term pioneer islands. However, it will be interesting to observe whether any of the 2014 pioneer islands (deposited on 6\textsuperscript{th} November) are able to survive in the longer term, given the relatively low flows since their deposition (Figure 2).

Information gained from the field campaigns in 2016 and 2017 provides indications of the potential importance of several processes in island development. Between these two field campaigns, there were three small flood events on 14\textsuperscript{th} July, 6\textsuperscript{th} and 19\textsuperscript{th} November 2016 (Figure 9), with a maximum water elevation of 0.25m (detrended elevation) on 14\textsuperscript{th} July 2016. This maximum elevation would have inundated all unvegetated surfaces and most of the 2014PI, 2004PI and 2004btwn surfaces (Figure 3). The vegetation cover on the latter three surfaces (2014PI, 2004PI, 2004btwn) is likely to have retained sediment from these floods as they receded, and since the floods are relatively small, the transported sediment is likely to have been quite fine, partly explaining the sediment fining on these surfaces between the two sampling campaigns (Figure 5). However, these flood events cannot explain sediment fining on higher surfaces. Gurnell et al. (2008) proposed wind storms as being another important mechanism for transporting sediments along the Tagliamento river corridor that can be intercepted and deposited on vegetated surfaces. This proposal was founded on a unique sequence of events which resulted in the production of very fine surface crusts, whose properties suggested wind as the most likely transporting agent. Wind storms transporting dense dust particles are quite common on the Tagliamento and their importance may be underestimated on other braided rivers where vast areas of exposed sediments can provide fine sediment for wind transport. Between field campaigns, there was a wind speed maximum of 26.3 m/s on 13 July and a period from 8\textsuperscript{th} to 12\textsuperscript{th} November 2016 when daily maximum wind speeds exceeded 15 m/s, with a maximum of 23.1 m/s on 10\textsuperscript{th} November 2016. Moreover, almost no precipitation occurred in December 2016 and January 2017, whereas several days had a maximum wind speed larger than 10 m/s, suggesting dry conditions may have favoured wind transport. Wind transport may explain the deposition of
finer sediments on surfaces that were not inundated between the field campaigns, particularly as the wind-deposited crusts sampled by Gurnell et al. (2008) within the study reach had an average D90 grain size of 6.7 $\phi$, which compares favourably with the increases in D90 illustrated in Figure 5. These observations suggest that wind as well as water may play a role in the aggradation and fining of surface sediments as islands increase in age and surface elevation on the Tagliamento and possibly other braided rivers.

Finally, the winter seed bank data has some relevance for both short and long term processes of island development. It is unsurprising that there is low similarity between the species in the seedbank and established vegetation (Figure 7) as a lack of similarity has been observed in the riparian seed bank and standing vegetation of other river systems, which have also shown a high seasonal variability in seed bank composition (e.g. Gurnell et al., 2006, 2008). However, the lack of similarity between the winter seedbank and vegetation composition in the present study is particularly stark. Since the seed bank was sampled in winter, it is not surprising that it mainly contained species that are associated with a persistent seed bank (Figure 8C). However, there is evidence that at least some of the seed species that were sampled have been transported into the sampling locations. In particular, some aquatic species are present in the seed bank but not in the standing vegetation. Whilst this is not surprising given their habitat requirements (there are no water bodies on the islands and aquatic species are rarely found in the ponds adjacent to pioneer and established islands), their presence illustrates that they have been dispersed into the sampled surface sediments. Their most likely source is a tributary stream that enters the Tagliamento main stem at the upstream end of the study reach and supports a variety of aquatic plant species, or they may have arrived from other upstream water bodies. Although water transport may explain the presence of these seed species on the 2004PI and 2004btwn surfaces, their presence on higher surfaces (Figure 8D) cannot be explained by water transport but could be explained by remobilisation and deposition by wind. Both wind and water are recognised as important means of seed dispersal (Fenner and Thompson,
and both are likely to be associated with deposition of seeds on island surfaces by events that occur over periods of hours to days, transporting seeds from their source areas and also remobilising them from other parts of the river bed and margins. In addition, larger vegetative propagules may be transported and deposited by floods to add to living plants and propagules co-deposited with soils attached to uprooted, deposited trees. One final point that relates to both dispersal mechanisms and aggradation, is that the 2004 islands stand out as not only having the highest decadal aggradation rates (Figure 3); the highest seed abundance (Figure 6) and highest number of species (Figure 8A) in their seedbank; and a remarkable development in their standing vegetation (Figures 7 and 8); but in the short term (between 2016 and 2017 sampling) they were affected by both wind and water dispersal processes (Figure 9), enabling enhanced sediment delivery, surface aggradation and the delivery and retention of plant propagules from a wide variety of locations and thus a potentially substantial species pool. Such fine-scale patterns of propagule deposition and plant colonisation are likely to add to the complexity of island development and contribute to the shifting habitat mosaic found at multiple scales within the Tagliamento’s island-braided reaches (e.g. Ward et al., 2002a).

Management Applications and Concluding Remarks

The recognition of islands as important landscape elements that are indicative of river ecosystem function and health (Tockner et al., 2003; Beechie et al., 2006) has led to increased interest in incorporating such landforms and their underlying processes into river restoration and management efforts. For example, Wyrick and Klingeman (2011) note that despite their widespread occurrence and ecological importance, islands are rarely incorporated into river restoration concepts. They propose a process-based island classification scheme that can identify island types, their formative processes and the relationship between island formation and river processes in general. As Wyrick and Klingeman (2011) indicate, any incorporation of islands and island-building processes in
river restoration and management need to be cognizant of both the mechanisms and
timescales of development that we have begun to explore here. In particular, our data and
similar measurements from other river systems can contribute to the refinement and testing
of numerical models that are increasingly incorporating physically based
vegetation/morphology feedbacks and could provide important means of forecasting likely
evolutionary trajectories of vegetated landforms under different environmental conditions
(e.g. van Oorschot et al., 2016; Zen et al., 2016).

Gurnell et al. (2001, updated 2012, 2016) presented a conceptual model of island
development based on observations along the braided, gravel-bed Tagliamento River. Since
then, the expanding literature on river island development, has primarily focused on the
formative physical processes of island development, their morphological evolution,
sedimentary environments, or aspects of their ecology and biodiversity (e.g. Mikuš et al.
2013; Picco et al. 2015; Raška et al. 2016; Vanbergen et al., 2017). In this paper we have
integrated these different perspectives and considered them across different timescales.
Although the datasets are not as comprehensive as we would like, this is often the case with
ecological data in complex and dynamic ecosystems, but we nevertheless consider them
sufficient to provide valuable information on elements of island development where
knowledge is notably sparse.

First, we have provided support to the view that when islands are initiated by the sprouting of
deposited trees (the ‘regeneration from living wood’ pathway; Gurnell et al., 2001), the
elevation of the tree deposition site matters (see also Francis, 2007). Trees are only
uprooted, transported and deposited in sizeable numbers during relatively large flood events
(e.g. Comiti et al., 2016), with deposition occurring during the peak and falling limb of these
flood events (e.g. MacVicar et al., 2009). Depositionary location governs both water access
(the lower the elevation, the closer to the water table) and likelihood of disturbance and
removal prior to establishment (the higher the elevation, the less likely they will be
disturbed). Therefore, if trees are deposited at low elevation, where they have access to
water to support rapid growth, river flows in the first two to three years following deposition are critical to their survival. If no major floods occur in this early period after deposition the trees can develop significant root and shoot biomass to anchor them and enable them to trap transported sediments, increase their surface elevation and thus reduce the level of flow disturbance to which they are subsequently subjected. These early developmental processes and timeframes are likely to be applicable to all island braided rivers where island development is initiated by sprouting of uprooted trees, and highlight the importance of regenerating trees having sufficient access to water and limited fluvial disturbance during initial years of establishment if island formation is to be facilitated.

Second, we have shown that once early establishment has occurred, islands aggrade their surfaces and develop a vegetation canopy at a remarkably steady rate over a decadal time scale. As islands aggrade and above-ground vegetation biomass and canopy height increase, there is also a steady fining of surface sediments and an increase in their organic content, including living material such as roots and fungal hyphae. This steady development reflects the fact that the study reach is subject to groundwater upwelling and thus possesses a fairly consistent and reliable moisture supply to support growth of the main tree species driving island initiation and development along the Tagliamento: *Populus nigra*. Thus, in the case of the study reach, *P. nigra* acts as a true ecosystem engineer (Jones et al., 1994, Gurnell, 2014), and our observations are likely to be applicable to other river reaches where water table fluctuations operate within a relatively small range and where *Populus nigra* or other riparian Salicaceae that are similarly sensitive to moisture availability and groundwater depth are driving pioneer island development. In reaches where major water table fluctuations occur, survival of deposited trees will be more sensitive to the elevation at which they are deposited, as will their subsequent rate of establishment. The initial establishment and growth of islands and the development of their surface sediments and vegetation cover as well as their ability to withstand subsequent flood events will vary not only with the river flow regime but also with the groundwater regime (e.g. Bätz et al., 2016) and any
confounding climatic trends (low rainfall, high evaporation). Detailed analyses to compare
island and associated dynamics in reaches subject to different groundwater / water
availability conditions are needed to more fully investigate the integrated biological and
geomorphological implications for island evolution, and how this may relate to management
and restoration.

Third, we found the maximum number of plant species, seed bank species, and seed
abundance to be associated with island surfaces of intermediate age and elevation,
reflecting seral trajectories and patterns of disturbance. This further highlights the
importance of allogenic disturbances and complex dynamics that shape the ecology of
building islands, which may serve to confound easy prediction of, for example, plant
community development. In an early study, Nagel et al. (1980) observed that river islands
along the lower energy, regulated Platt River in Nebraska (USA) presented similar trends of
soil development and aggradation with island age, but also that although plant diversity and
abundance of perennials increased with island age, island communities remained broadly
similar and at early seral stages. Expectations around ecological development and
succession of river islands, for example if used an indicators of ecosystem health or in
restoration efforts, should therefore take into account the complexity of factors determining
assemblages, which will vary between reaches and river systems. In our case for example,
islands of intermediate age had a rather particular initiation and evolution history, and more
work would be needed to establish the transferability of our findings to other contexts.

Finally, our most speculative finding relates to the importance of climatic conditions in
influencing island evolution at event to seasonal timescales. We have observed significant
fining of surface sediments on all vegetated surfaces over a period of approximately six
months. Whereas some of this fining can be attributed to deposition of fine sediments
transported by small flood events on inundated vegetated surfaces, many of the surfaces
showing fining were not inundated. Based on earlier observations (Gurnell et al., 2008), we
have suggested wind as a potentially important agent for transporting fine sediments that
become trapped by vegetation, particularly during dry periods. Aeolian fine sediments and
dusts (including organic particulates) have been found to be more pervasive and ecologically
important in ecosystems than usually assumed, for example contributing to river nutrient
loads, especially in more arid basins (e.g. McTainsh and Strong 2007). McGowan et al.
(1996) note that dust entrainment may be particularly prevalent along alpine river valleys,
where the topography can channel high wind speeds. On the study reach and higher up the
river, fine deposits on exposed bars, especially at high elevations, may represent a source of
fine sediments that become trapped by vegetation. Wind is also recognised as a major agent
for seed transport; most notably in the present context for the transport of the abundant
short-lived seeds of the Salicaceae, alongside and in combination with water (e.g. Boland
2014, 2017). Wind may therefore have agency in island aggradation and also the delivery of
seeds from terrestrial and riparian species pools, though further work is needed to confirm
this. Furthermore, we have provided some support for a potentially important role of
temperature conditions in the annual cycle of vegetation development and flowering.
Species which only show above-ground biomass seasonally could be an important influence
on seasonal fine sediment trapping and retention of surface moisture through the late spring
and summer months. Thus, while flood and low flow events are clearly the key controls on
island evolution, various climatic variables may be extremely important for fine sediment
retention, soil development and other short term facets of island evolution, and should be
considered in any management or restoration context. However, more research is needed to
verify and quantify these influences

ACKNOWLEDGMENTS

Figure 1 includes two images from Google Earth, both from the same supplier: Image ©
2017 DigitalGlobe. In using these images, we have conformed to guidelines available from
http://www.google.com/permissions/geoguidelines/attr-guide.html (accessed 16 December
2017) including image attributions in the Figure caption that conform to ‘the text of your
For Peer Review

attribution must say the name “Google” and the relevant data provider(s), such as “Map data: Google, DigitalGlobe” and we have not obtained written permission to use these images because the guidelines state that ‘Due to limited resources and high demand, we’re unable to sign any letter or contract specifying that your project or use has our explicit permission’. The authors acknowledge the UK Natural Environment Research Council for providing the 2005 lidar data; Nicola Surian, University of Padova (CARIPARO project) for the 2010 lidar data; and Yasuhiro Takemon, University of Kyoto for the 2013 lidar data. Ulfah Mardhiah’s research was funded by the SMART Joint Doctoral Programme (Science for Management of Rivers and their Tidal systems), which is financed by the Erasmus Mundus Programme of the European Union. We thank C. Cruciat, S. Arcandi, M. Benvegnù and M. Welber for helping during the field data collection.

REFERENCES


Belletti B, Dufour S, Piégay H. 2014. Regional assessment of multidecadal changes in braided riverscapes following large floods (example of 12 reaches in south east of France). Advances in Geosciences, 37: 57-71


Mardhiah U, Caruso T, Gurnell AM, Rillig MC. 2014. Just a matter of time: Fungi and roots significantly and rapidly aggregate soil over four decades along the Tagliamento River, NE Italy. Soil Biology and Biochemistry, 75: 133-142.


For Peer Review


**FIGURE UNDERLINES**

Figure 1. Distribution of sampling locations used in 2016 and 2017 according to date of surface initiation, overlain on images of the study reach captured in 2002 and 2015. The images are overlain with coordinates for WGS84 UTM zone 33 to indicate the study area location. Images were obtained from Google Earth, Image © 2017 DigitalGlobe, and were captured on 21 July 2002 and 12 July 2015.

Figure 2. Data sets and events described in this paper in relation to variations in water level in the study reach between January 2000 and February 2017 inclusive.
Figure 3. Water level (detrended elevation in m) - frequency relationship in the study reach estimated for the period 2000-2017, compared with the interquartile range of the detrended elevation of sampling locations on 1980EI, 2000PI, 2000btwn, 2004PI, 2004btwn surfaces in 2005, 2010 and 2013 and the maximum river stage between June 2016 and February 2017 sampling campaigns.

Figure 4. Surface sediment sampling locations and times plotted in relation to their scores on the first two PCs of a PCA. The PCA was applied to the %organic, D50, %gravel, %sand, %silt, %clay content of each sample: (iii) illustrates the loadings of these six variables on the first two PCs. The samples are coded according to (i) the sampled surface, (ii) the survey year, (iv) sediment class (derived from AHC of %organic, D50, %gravel, %sand, %silt, %clay), (v) surface age at the time of sampling.

Figure 5. A, B, C, D: Particle size distributions for the <1 mm (0 ϕ) fraction of island surface (A, B) and unvegetated and between island (CD) surface sediment samples obtained in June 2016 (A,C) and February 2017 (B,D). The data are presented as percentages of the sample within 1 ϕ bins (<1, 1-2, 2-3, ..., 10-11, >11 ϕ). E, F, G: D10, D50 and D90 percentile particle sizes estimated for the 139 distributions contributing to the averages shown in A, B, C, D. Note that some D10 estimates are larger (<0 ϕ) because the <1 ϕ bin contains such a large percentage of the particles in these coarse samples.

Figure 7. Similarity in the species composition of the standing vegetation (July 2011, June 2016) and seed bank (February 2011) observed on surfaces of different type and age.

Agglomerative Hierarchical Cluster analysis was performed with the Jaccard coefficient as the similarity measure and clustering determined using the unweighted pair group average.

Figure 8. Standing vegetation and seed bank species composition on surfaces of different age, based on surveys of the standing vegetation in 2011 and 2016, and the winter seed bank in 2017. A. Number of species present, B. Average C, S, R scores, C. Proportions of species with long-term persistent, short-term persistent, and transient seed banks, D. Proportions of different most common terminal habitats

Figure 9. Daily total precipitation, maximum wind speed, and maximum detrended water level between field campaigns in June 2016 and February 2017.

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>F-value</th>
<th>P-value</th>
<th>Bonferroni pairwise comparisons (P&lt;0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bed elevation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface</td>
<td>4</td>
<td>77.60</td>
<td>&lt;0.001</td>
<td>1980EI &gt; 2000PI, 2000btwn &gt; 2004PI, 2004btwn</td>
</tr>
<tr>
<td>Lidar date</td>
<td>2</td>
<td>3.55</td>
<td>0.031</td>
<td>2013, 2010 &gt; 2005</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>R² (adjusted) = 65.8%</td>
</tr>
<tr>
<td><strong>Vegetation Canopy</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lidar date</td>
<td>2</td>
<td>64.24</td>
<td>&lt;0.001</td>
<td>2013 &gt; 2010 &gt; 2005</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>R² (adjusted) = 96.36%</td>
</tr>
</tbody>
</table>
Table 2. Centroid values for sediment classes discriminated using AHC (Euclidean distance, Ward’s clustering algorithm) applied to six sediment properties of 139 surface sediment samples, with significant differences between classes in relation to the six contributing sediment properties (Kruskal Wallis tests).

<table>
<thead>
<tr>
<th>Sample size and sediment property</th>
<th>A mainly gravel</th>
<th>B gravel-sand</th>
<th>C sand-gravel</th>
<th>D mainly sand (notable organic)</th>
<th>E sand with some silt (notable organic)</th>
<th>F sand-silt (notable organic and clay)</th>
<th>Significant differences between classes*</th>
</tr>
</thead>
<tbody>
<tr>
<td>sample size</td>
<td>23</td>
<td>25</td>
<td>16</td>
<td>36</td>
<td>28</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>%organic</td>
<td>0.3</td>
<td>0.8</td>
<td>1.4</td>
<td>5.0</td>
<td>4.8</td>
<td>6.0</td>
<td>D,E,F &gt; A,B, C&gt;A</td>
</tr>
<tr>
<td>D50((\phi))</td>
<td>-1.4</td>
<td>-1.7</td>
<td>1.3</td>
<td>2.1</td>
<td>2.9</td>
<td>3.7</td>
<td>E,F &gt; C,D, A,B</td>
</tr>
<tr>
<td>%gravel</td>
<td>80.6</td>
<td>58.5</td>
<td>26.3</td>
<td>0.5</td>
<td>0.4</td>
<td>0.1</td>
<td>A,B,C,D,E,F,A,C</td>
</tr>
<tr>
<td>%sand</td>
<td>19.0</td>
<td>38.5</td>
<td>64.9</td>
<td>91.0</td>
<td>76.8</td>
<td>59.8</td>
<td>C,D,E,F &gt; A,B, D&gt;C,F</td>
</tr>
<tr>
<td>%silt</td>
<td>0.5</td>
<td>2.9</td>
<td>8.4</td>
<td>8.4</td>
<td>21.7</td>
<td>37.5</td>
<td>E,F &gt; B,C,D,A, C,D&gt;B</td>
</tr>
<tr>
<td>%clay</td>
<td>0.0</td>
<td>0.1</td>
<td>0.4</td>
<td>0.1</td>
<td>1.2</td>
<td>2.7</td>
<td>E,F &gt; A,B, C,D</td>
</tr>
</tbody>
</table>

* Kruskal Wallis tests, df = 5, P < 0.0001, multiple pairwise comparisons using Dunn’s procedure with Bonferroni corrected significance level (P = 0.003)
Table 3. Eigenvalues, percentage variability explained, and variable loadings on the first three Principal Components of a PCA applied to six sediment properties of 139 surface sediment samples.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>4.371</td>
<td>1.201</td>
<td>0.197</td>
</tr>
<tr>
<td>Variability (%)</td>
<td>72.843</td>
<td>20.010</td>
<td>3.282</td>
</tr>
<tr>
<td>Cumulative %</td>
<td>72.843</td>
<td>92.854</td>
<td>96.136</td>
</tr>
<tr>
<td>Loadings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%organic</td>
<td>0.921</td>
<td>0.157</td>
<td>-0.336</td>
</tr>
<tr>
<td>D50(ϕ)</td>
<td>0.946</td>
<td>-0.123</td>
<td>0.161</td>
</tr>
<tr>
<td>%gravel</td>
<td>-0.937</td>
<td>-0.280</td>
<td>0.001</td>
</tr>
<tr>
<td>%sand</td>
<td>0.568</td>
<td>0.790</td>
<td>0.182</td>
</tr>
<tr>
<td>%silt</td>
<td>0.926</td>
<td>-0.304</td>
<td>-0.059</td>
</tr>
<tr>
<td>%clay</td>
<td>0.754</td>
<td>-0.605</td>
<td>0.146</td>
</tr>
</tbody>
</table>
Table 4. Generalised linear models for each of the ten, fifty and ninety percentiles (D10, D50, D90) of the 0 $\phi$ and finer mineral sediment fraction of 139 particle size distributions, with sampling year (2016, 2017), surface (1980EI, 2000PI, 2000btwn, 2004PI, 2004btwn, 2014PI, unveg) and interactions between year and surface as the explanatory variables (percentile expressed in $\phi$ units, statistical significance of differences between groups explored using the Bonferroni method).

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>F-value</th>
<th>P-value</th>
<th>Bonferroni pairwise comparisons (P&lt;0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>D10</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface</td>
<td>6</td>
<td>44.27</td>
<td>&lt;0.001</td>
<td>1980EI, 2000PI, 2004PI &gt; 2014PI, 2000btwn &gt; 2004btwn, unveg</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>8.51</td>
<td>0.004</td>
<td>2017 &gt; 2016</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$R^2$ (adjusted) = 66.8%</td>
</tr>
<tr>
<td><strong>D50</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface</td>
<td>6</td>
<td>35.11</td>
<td>&lt;0.001</td>
<td>1980EI, 2000PI, 2004PI &gt; 2014PI, 2000btwn &gt; 2004btwn, unveg</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>8.88</td>
<td>0.003</td>
<td>2017 &gt; 2016</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$R^2$ (adjusted) = 60.6%</td>
</tr>
<tr>
<td><strong>D90</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface</td>
<td>6</td>
<td>26.00</td>
<td>&lt;0.001</td>
<td>1980EI, 2000PI, 2004PI &gt; 2000btwn, 2004btwn &gt; unveg</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>9.37</td>
<td>0.003</td>
<td>2017 &gt; 2016</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$R^2$ (adjusted) = 57.2%</td>
</tr>
</tbody>
</table>
Figure 1. Distribution of sampling locations used in 2016 and 2017 according to date of surface initiation, overlain on images of the study reach captured in 2002 and 2015. The images are overlain with coordinates for WGS84 UTM zone 33 to indicate the study area location. Images were obtained from Google Earth, Image © 2017 DigitalGlobe, and were captured on 21 July 2002 and 12 July 2015.

113x122mm (300 x 300 DPI)
Figure 2. Data sets and events described in this paper in relation to variations in water level in the study reach between January 2000 and February 2017 inclusive.
Figure 3. Water level (detrended elevation in m) - frequency relationship in the study reach estimated for the period 2000-2017, compared with the interquartile range of the detrended elevation of sampling locations on 1980EI, 2000PI, 2000btwn, 2004PI, 2004btwn surfaces in 2005, 2010 and 2013 and the maximum river stage between June 2016 and February 2017 sampling campaigns.
Figure 4. Sediment sampling locations and times plotted in relation to their scores on the first two PCs of a PCA. The PCA was applied to the %organic, D50, %gravel, %sand, %silt, %clay content of each sample: (iii) illustrates the loadings of these six variables on the first two PCs. The samples are coded according to (i) the sampled surface, (ii) the survey year, (iv) sediment class (derived from AHC of %organic, D50, %gravel, %sand, %silt, %clay), (v) surface age at the time of sampling.
For Peer Review

Figure 5. A, B, C, D: Particle size distributions for the <1 mm (0 φ) fraction of island surface (A, B) and unvegetated and between island (C, D) sediment samples obtained in June 2016 (A,C) and February 2017 (B,D). The data are presented as percentages of the sample within 1 φ bins (<1, 1-2, 2-3, ..., 10-11, >11 φ).

E, F, G: D10, D50 and D90 percentile particle sizes estimated for the 139 distributions contributing to the averages shown in A, B, C, D. Note that some D10 estimates are larger (<0 φ) because the <1 φ bin contains such a large percentage of the particles in these coarse samples.

168x173mm (300 x 300 DPI)

94x69mm (300 x 300 DPI)
Figure 7. Similarity in the species composition of the standing vegetation (July 2011, June 2016) and seed bank (February 2011) observed on surfaces of different type and age. Agglomerative Hierarchical Cluster analysis was performed with the Jaccard coefficient as the similarity measure and clustering determined using the unweighted pair group average.

104x108mm (300 x 300 DPI)
Figure 8. Standing vegetation and seed bank species composition on surfaces of different age, based on surveys of the standing vegetation in 2011 and 2016, and the winter seed bank in 2017. A. Number of species present, B. Average C, S, R scores, C. Proportions of species with long-term persistent, short-term persistent, and transient seed banks, D. Proportions of different most common terminal habitats.
Figure 9. Daily total precipitation, maximum wind speed, and maximum detrended water level between field campaigns in June 2016 and February 2017.

119x121mm (300 x 300 DPI)