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RESEARCH ARTICLE

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Extending the conceptual model of river island development to incorporate different tree species and environmental conditions

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Abstract

Riparian vegetation survival and establishment in gravel-bed rivers depends on the balance between vegetation growth and flood disturbance. We present four examples of vegetation and landform development in gaps (linear open spaces) between established islands and/or floodplain within a reach of the middle Tagliamento River, Italy. Gaps offer shelter to vegetation, supporting higher colonization success and different vegetation-landform evolution pathways. Time sequences of aerial images track vegetation development over 30 years in the four gaps. In combination with the flood disturbance time series, we interpret vegetation dynamics and identify the fate of sexual and asexual reproduction strategies by observing vegetation expansion from lines of young plants and shrubs and from uprooted deposited trees and pioneer islands, respectively. Analysis of image sequences reveals common features across the four gaps that are generalized to extend a conceptual model of island development. Growing conditions, disturbance energy and time (window of opportunity) between major floods are the main controls on vegetation colonization. These vary among rivers, among reaches along the same river and locally, as in the investigated gaps, allowing different tree species with different life history traits (e.g., *Populus nigra*, *Alnus incana*) to engineer local river landforms in different and complementary ways. Although the conceptual model is inspired by observations on the Tagliamento River, consideration of species life history traits and the joint influences of growing conditions, disturbance energy and windows of opportunity provide a framework that may be applied to other temperate rivers where trees drive landform development.

KEYWORDS

Alnus incana, disturbance energy, island development, physical ecosystem engineering, *Populus nigra*, riparian vegetation

1 | INTRODUCTION

The importance of riparian trees for the development and stability of river islands and floodplain margins has been a subject of considerable research attention, especially over the last two decades. Building on understanding of vegetation colonization of disturbed, dynamic riparian zones (e.g., Bornette, Tabacchi, Hupp, Puijalon, & Rostan, 2008; Dykaar & Wigington, 2000; Johnson, 2000; Mahoney & Rood, 1998;

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Polzin & Rood, 2006) increasing emphasis has been placed on feedbacks between plants and fluvial processes (Dufour, Rodríguez-González, & Laslier, 2019) and particularly the ways in which plant species may act as "physical ecosystem engineers" (Jones, Lawton, & Shachak, 1997), driving the creation and maintenance of fluvial landforms (e.g., Bendix & Stella, 2013; Bertoldi, Gurnell, & Drake, 2011; Corenblit et al., 2011, 2015; Corenblit, Steiger, Gurnell, Tabacchi, & Roques, 2009; Corenblit, Tabacchi, Steiger, & Gurnell, 2007; Gurnell, 2014; Gurnell et al., 2016; Gurnell, Bertoldi, & Corenblit, 2012; Kollmann, Vieli, Edwards, Tockner, & Ward, 1999; Politti, Bertoldi, Gurnell, & Henshaw, 2018; Tabacchi et al., 2019).

Research over two decades on the Tagliamento River, N.E. Italy, has concentrated on such plant—physical environment interactions. The physical roles of species from the Salicaceae family have been investigated, particularly *Populus nigra* L. (black poplar), which dominates islands and floodplain margins along the middle and lower reaches of the river. This research led to the proposal of a conceptual model of island development, whereby species from the Salicaceae family drive island development (Gurnell et al., 2001; Gurnell & Petts, 2002; Gurnell, Tockner, Edwards, & Petts, 2005). The conceptual model incorporates three pathways along which Salicaceae species may colonize the surfaces of river bars and initiate island development: (1) germination and growth of widely dispersed seeds when they are deposited at suitable germination sites; (2) germination and growth of seeds that accumulate in sheltered locations such as in the lee of wood piles and (3) sprouting of shoots and roots from deposited wood pieces or entire uprooted trees. However, in the high-energy context of the Tagliamento, Pathway (3) has been identified as the most likely to initiate island development with the rapid rooting and sprouting of flood-deposited trees and large wood playing a crucial role in stabilizing bar surfaces and trapping fluvial sediments, wood and plant propagules to construct small "pioneer" islands (Edwards et al., 1999). Pioneer islands provide shelter for further vegetation development and sediment retention, and they may coalesce to form larger, building islands and extensions of the floodplain. Gurnell and Petts (2006) extended the conceptual model by incorporating the impacts of changes in flood unit stream power and also the depth and variability of the alluvial water table along narrowing and widening sections of a river. Such longitudinal changes in the balance between flood disturbance severity and the growth performance of young trees in response to the local groundwater regime explains observed longitudinal changes in the presence, spatial extent and persistence of islands within different reaches of the Tagliamento. In particular, Gurnell and Petts (2006) emphasized reach-scale variations in the potential of Pathway (3) to support pioneer and building island development following the deposition of uprooted trees and large wood pieces of Salicaceae species.

The "recruitment box" model (Mahoney & Rood, 1998) is relevant to Pathways (1) and (2) of the island development model. It couples (a) the seasonal production of seeds by riparian Salicaceae species with (b) synchronous seed dispersal by floods to suitable germination sites and then (c) rapid seedling growth promoted by post-flood declines in the water table during a period without significant flood disturbance. This model has been widely applied and much research has developed from it to explain the frequent presence of single species, single age cohorts of Salicaceae species bordering many rivers and, more generally, how such riparian systems function and can be conserved (e.g., Braatne, Jamieson, Gill, & Rood, 2007; Cooper, Merritt, Andersen, & Chimner, 1999; Foster & Rood, 2017; Kalischuk, Rood, & Mahoney, 2001; Lytle & Merritt, 2004; Scott, Auble, Dixon, Johnson, & Rabbe, 2013; Scott, Auble, & Friedman, 1997). However, growth from seedlings or small vegetative fragments do not appear to be a major driver of the first stages of tree colonization along the middle and lower Tagliamento main stem. Even in the upper part of the main stem, where sprouting of vegetative fragments deposited on the river bed is relatively rare, accumulations of large wood and/or boulders are crucial for providing shelter within which seedlings (notably of the locally co-dominant species *A. incana*) survive and initiate pioneer islands (Pathway (2), Gurnell et al., 2001). The relative lack of effectiveness of sexual reproductive Pathways (1) and (2) for initiating vegetation establishment and landform development in the middle and lower Tagliamento has been attributed to (a) slower early growth rates of seedlings in comparison with sprouts from vegetative propagules of varying size, particularly from uprooted, deposited trees (Francis, 2007; Francis & Gurnell, 2006; Gurnell, 2016; Moggridge & Gurnell, 2009), (b) frequent "flashy" flood disturbances capable of uprooting or burying seedlings and (c) the predominant occurrence of the largest floods in autumn and thus well beyond the spring season of seed production by *P. nigra* and other species from the Salicaceae family that are present along the river (Karrenberg & Suter, 2003). Point (c) is particularly important because seeds of the riparian Salicaceae have an extremely short period of viability (Gosling, 2007; Karrenberg & Suter, 2003). However, this is not such a limiting factor for dispersal and successful establishment of species that produce seeds with a longer period of viability or that reproduce asexually. For these species, flood timing does not strongly limit successful recruitment from propagules that are dispersed to suitable germination or sprouting sites, but the length of time without disturbance or "window of opportunity" (Balke, Herman, & Bouma, 2014) for growth following flood dispersal remains a major control on recruitment success.

Recently, Bertoldi and Gurnell (2020) reported on the potential contribution of *A. incana* (L.) Moench. (grey alder), a member of the Betulaceae family that produces seeds with a longer period of viability than the riparian Salicaceae, for river bed landform development in the middle reaches of the Tagliamento. They investigated broad spatio-temporal and topographic changes across the river bed associated with woody vegetation in general (dominated by *P. nigra*) and with *A. incana* in particular. Over the last two decades within a >7 km long study reach, *A. incana* has shown an expansion in cover; is mainly distributed in lines that broadly parallel the river's course; is located at lower elevations on the river bed than riparian woodland vegetation in general; and is associated with local aggradation of the river bed. These observations indicate that in addition to general aggradation and expansion of wooded islands dominated by *P. nigra*, *A. incana* also appears to be driving island development locally along the

margins of some channels, bars and islands. Additionally, Bertoldi and Gurnell (2020) concluded that an increase in cover of *A. incana* since 2000 is most likely explained by the species' presence at relatively lower elevations than vegetated areas in general and along landform edges that would be preferentially eroded by major floods. Therefore, the recent apparent increase in the cover of *A. incana* does not seem to relate to an extension of the species' geographical range but rather recovery of the species following the largest flood in the last 35 years in 2000. This conclusion is supported by Lippert, Müller, Rossel, Schauer, and Vetter (1995) and Karrenberg, Kollmann, Edwards, Gurnell, and Petts (2003), who record significant presence of *A. incana* in the middle reaches of the Tagliamento prior to the 2000 flood. In short, *A. incana* appears to be associated with landform building in specific locations where it may complement physical engineering by the dominant species *P. nigra*, and its importance may vary through time because of its greater susceptibility to removal during large floods.

Following from this previous research, we investigate the potential complementary role of *A. incana* (Betulaceae) to that of the dominant species, *P. nigra* (Salicaceae), in physically engineering the development of islands and floodplains along the middle reaches of the Tagliamento. Like *P. nigra*, *A. incana* is a pioneer species that can rapidly colonize areas of bare ground. However unlike *P. nigra*, *A. incana* (a) releases seeds in the autumn (Wilson, Mason, Savill, & Jinks, 2018) that are easy to store (Gosling, 2007) with some evidence (Thompson, Bakker, & Bekker, 1997) that the seeds form a short-term persistent seed bank (i.e., can remain viable for at least 1 year), ensuring viable seeds are available throughout the year for redistribution by floods; (b) is less likely to reproduce asexually (as noted on the Tagliamento by Kollmann et al., 1999, and experimentally by Francis, Gurnell, Petts, & Edwards, 2005), although flood damage may encourage sucker and root stump shoots in a similar manner to that reported for regrowth following coppicing (Rytter, 1996; Rytter, Sennerby-Forsse, & Alriksson, 2000; Wilson et al., 2018), and very occasionally some uprooted stumps may survive and sprout if deposited at suitable sites (authors' field observations) and (c) prefers moister, more nutrient-rich sites (Rytter, 1996). Thus, the two species show important differences in their life history traits and environmental requirements, which may allow some complementarity in their roles as physical ecosystem engineers.

In order to explore the potential physical ecosystem engineering role of *A. incana* in comparison with (*P. nigra*-dominated) vegetation in general, we investigate detailed pathways of vegetation establishment and landform building within gaps (linear open spaces) of varying width on the river bed of a reach of the middle Tagliamento River between areas of established vegetation (i.e., islands, floodplain). Gaps provide reduced local exposure of the bed to disturbance from floods and allow us to explore the following working hypotheses:

1. A reduction in exposure to flood disturbance (represented by areas of river bed confined within gaps) enhances the relative importance of sexual reproduction in the initiation of areas of woody vegetation on the river bed.
2. Vegetated area initiation and development displays distinctive spatio-temporal patterns reflecting traits of the colonizing woody species.
3. Patterns of vegetation and related landform development reflect the survival and growth of woody species under the influence of local growing conditions, flood disturbance energy and windows of opportunity between disturbances.

We generalize the outcomes of the above investigations to extend the conceptual "island development model" described by Gurnell et al., 2001 and Gurnell & Petts, 2006.

2 | METHODS

2.1 | Investigative design

Bertoldi and Gurnell (2020) present a spatio-temporal and topographic analysis of vegetation development across the three most heavily vegetated areas of the braid plain, totalling almost 1 km^2 area, of the river bed within an island-braided reach of the middle Tagliamento River (Figure 1a). To explore our three working hypotheses, we searched this surveyed area for gaps (linear spaces between established islands and or floodplain) that were oriented parallel to the braid plain (i.e., similar orientation to flood flows). We identified nine suitable gaps from which we selected three of contrasting width (Figure 1a, Gaps 1, 3 and 4). We added a fourth gap (Figure 1a, Gap 2) surveyed in the field in 2018, which had been removed by a flood prior to the above survey but was of intermediate width between Gap 1 and Gaps 3 and 4. Gaps of similar orientation with respect to flow, bounded by consistently high (wooded) boundary resistance but of different width are likely to moderate flood energy to different degrees, providing an energy gradient for investigating vegetation responses.

We assembled secondary data sources (river stage records, historical aerial images and airborne lidar data sets) and field observations for each gap. These supported definition of gap boundaries and underpinned reconstruction of vegetation and topographic development of the river bed (see Section 2.2).

The above analyses allow us to revisit our three working hypotheses and incorporate them into an extended conceptual model of island development (Gurnell et al., 2001; Gurnell & Petts, 2006).

2.2 | Secondary data sources

A 35 year river stage record (Figure 1b) from a site approximately 1 km downstream of the study reach illustrates the timing, magnitude and frequency of flood events. Black and grey arrows (Figure 1b) indicate all flood peaks exceeding 3 m stage (i.e., bankfull discharge: Bertoldi et al., 2009). Note that prior to 2000, stage was recorded irregularly but since 2000 measurements are at 30 min intervals. Flood events during 1990, 1996, 2000 and 2004 (black arrows) are

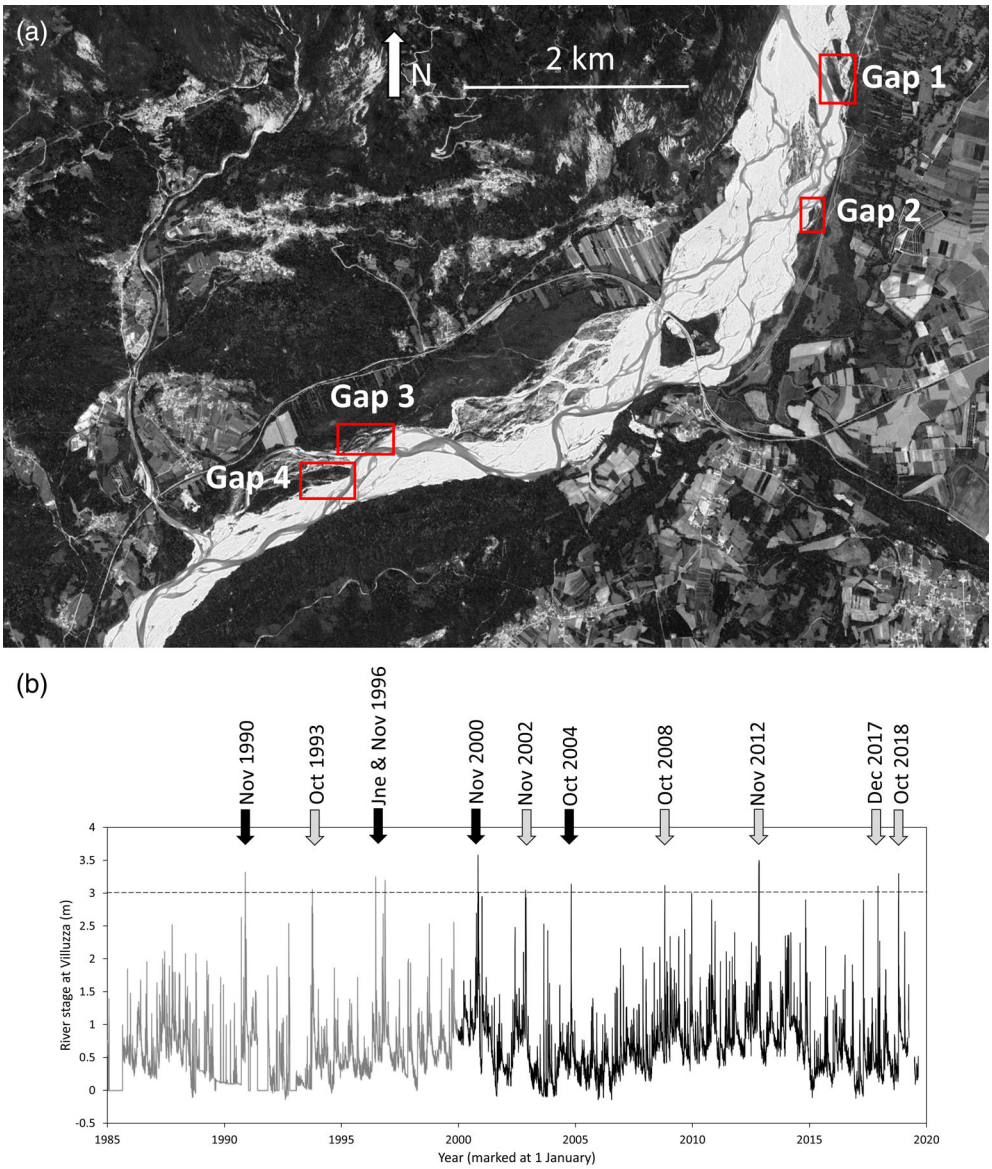


FIGURE 1 (a) The study reach showing Gaps 1, 2, 3 and 4. (The image was downloaded from Google Earth, image©2019 Maxar Technologies and flow is from North East (top right) to South West (bottom left); the centre of the braid plain extends from approximately 46.242075°N, 13.039804°E [upstream] to 46.192989°N, 12.961997°E [downstream].) (b) Daily river stage record at the Villuzza station (located 1 km downstream from the study reach), 1985 to present. The record after 2000 (black line) represents the daily maximum stage extracted from 30 min observations. The precise nature of the record before 2000 (grey line) is unknown but probably varies between single observations within a day and the highest observation within a day (the number of observations within a day is highly variable). Arrows indicate floods exceeding the approximate level of bankfull (stage = 3 m) with black arrows denoting the four floods discussed in detail and grey arrows denoting other floods with a stage exceeding 3 m [Colour figure can be viewed at wileyonlinelibrary.com]

the most relevant to our analysis because they are sufficiently old to assess the flood origins of trees that were both taller than 4 m during our field surveys in 2018 and 2019 (see below) and are also readily detected by the most recent airborne lidar data (2013, see below). Only one of these flood events (June 1996) did not occur in Autumn but this was followed by another of similar peak magnitude in November 1996. The four later bankfull events (2008, 2012, 2017 2018) also all occurred in autumn or winter. The 4 year "window of opportunity" without any significant floods between the October 2004 and October 2008 floods is also relevant to the following analyses. Later "windows" (2008–2012, 2012–2017) were not investigated because, following the above criteria, they are too recent to be investigated using the available secondary data sources, and, unlike 2004–2008, both were interrupted by near-bankfull events (Figure 1b).

Rectified aerial images (1986, 1993, 1997, 2003, 2005, 2010, 2011, 2013 2017) visualize the distribution and cover of bars, channels and vegetation over 30 years. The 1993 images were captured before the 1993 flood event. The first five image dates show the river before, between and after the 1990, 1996, 2000 and 2004 floods and the remaining dates capture later changes in land cover. The images were used to identifying gap boundaries and quantifying gap widths at times when the gaps were clearly defined and free of vegetation, particularly using the 2003 images, which were captured shortly after the largest flood in the last 35 years (in 2000). They also supported mapping of the changing distributions of flowing channels, areas of bare (unvegetated) river bed and established vegetation, and the locations of uprooted deposited trees, pioneer islands, lines of seedlings, lines of shrubs and any major accumulations of wood within and around each gap. While lines of young plants or shrubs may represent sprouting vegetative fragments deposited within flood trash lines, they are highly likely to represent growth from water-transported and deposited seeds and thus a sexual pathway to vegetation development. Therefore, lines of very young plants are

hereafter called "lines of seedlings." In contrast, uprooted, deposited trees and the pioneer islands that develop from them represent an asexual pathway to vegetation development.

Three airborne lidar surveys (May 2005, August 2010, October 2013) revealed changes in bed topography and the spatial extent and height of (*P. nigra* dominated) woody vegetation in general and also of field-mapped (see Section 2.3) *A. incana* individuals within and around the four gaps over an 8 year period.

2.3 | Field observations

In March 2019, the positions of all *A. incana* individuals taller than 4 m were recorded in and around Gaps 1, 3 and 4. Although the vegetation in Gap 2 and much of the adjacent island were removed by the October 2018 flood (Figure 1b), detailed field mapping and photography of the upstream half of this gap was undertaken in 2018. This provided a detailed pre-flood record of bed morphology, the distribution of woody vegetation and the main tree species, and also the locations of a sample of alder individuals taller than 4 m, allowing their changing height to be extracted from the three lidar surveys.

Bertoldi and Gurnell (2020) detail the analysis of lidar data to establish a typical annual vertical growth increment of approximately 0.6 m for *A. incana* within the study reach and its verification using field measurements.

3 | RESULTS

3.1 | Gap boundaries and widths

The boundaries of Gaps 1, 2, 3 and 4 (Figures 2–7) were established from aerial images. Each gap boundary was interpreted from the image which showed it at its widest extent and free of vegetation. Boundaries of Gaps 2, 3 and 4 were defined from the 2003 images. Although these gaps were present in earlier images, the largest

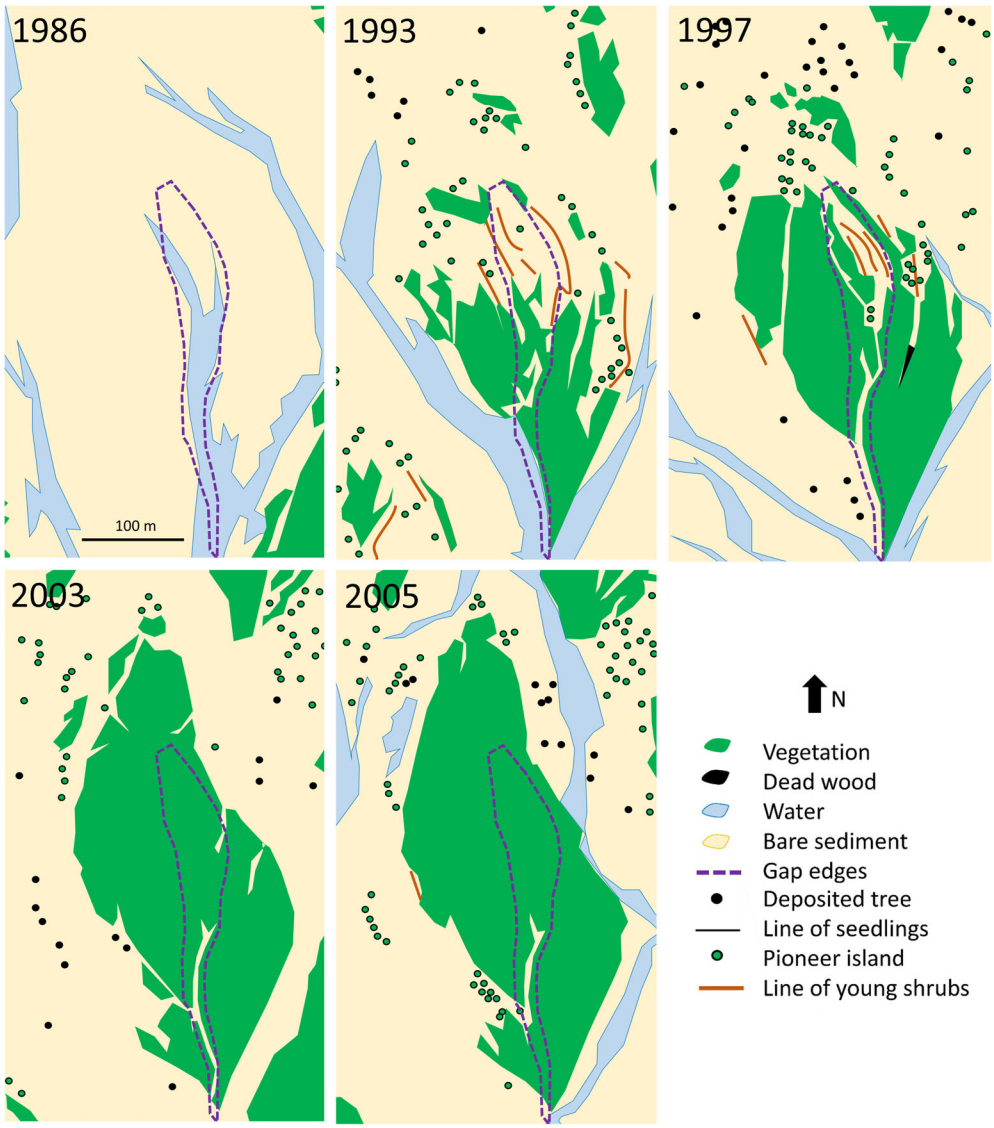


FIGURE 2 Maps of the distribution of cover types and vegetation features in and around Gap 1 interpreted from aerial images captured in 1986, 1993, 1997, 2003 and 2005 (note that the boundaries of the gap were inferred mainly from the 1993, 1997 and 2003 images plus the 2005 DEM (Figure 4) and that the gap is completely obscured (overhung) by vegetation in all images after 2005, flow is from north to south) [Colour figure can be viewed at wileyonlinelibrary.com]

flood on record in 2000 eroded extensive parts of their margins and all three gaps were free of vegetation in 2003. The 2000 flood does not appear to have affected the extent of Gap 1, which is marked by a river channel in the 1986 image. The relatively wide time spacing between early images and the fact that Gap 1 is the narrowest of the four and so its margins are often obscured (overhung) by vegetation, make tracking of its dimensions challenging. A composite approach involving inspection of early images and the earliest (2005) DEM was used to define the approximate boundaries of Gap 1, and may have defined a wider gap than is appropriate. Average gap widths of 27, 45, 98 and 97 m, respectively, for Gaps 1, 2, 3 and 4 were calculated from 10 equally spaced width measurements distributed along and perpendicular to each gap's upstream to downstream axis,.

3.2 | Evolution of vegetation cover and bed morphology in Gaps 1, 2, 3 and 4

Flowing channels, vegetated areas, areas of unvegetated sediment, deposited trees, pioneer islands, lines of seedlings and lines of young shrubs were mapped using the historical aerial images. Deposited trees and pioneer islands indicate the fate of large vegetative woody plant propagules, whereas lines of seedlings and shrubs predominantly indicate the fate of seeds and possibly small vegetative woody plant propagules deposited in flood trash lines. Time sequences of maps of these cover features are provided, respectively, for Gaps 1, 2, 3 and 4 in Figures 2, 3, 5 and 6. Figures 4 and 7 display detrended 2005 and 2013 DEMs and the distribution and relative height of vegetation in 2013 for Gaps 1 and 2 (Figure 4) and Gaps 3 and 4 (Figure 7).

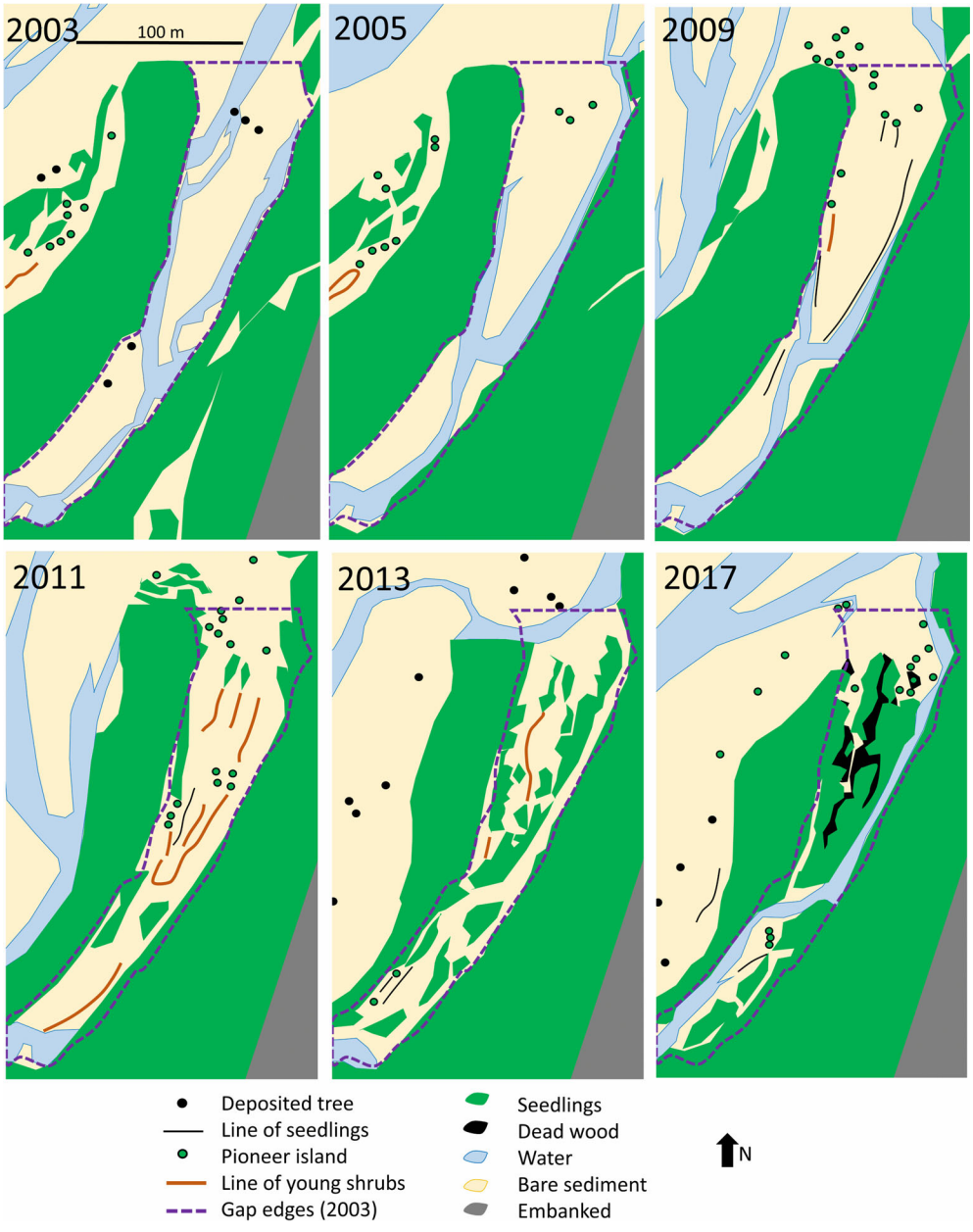


FIGURE 3 Maps of the distribution of cover types and vegetation features in and around Gap 2 interpreted from aerial images captured in 2003, 2005, 2009, 2011, 2013 and 2017 (flow is from north-east to south-west) [Colour figure can be viewed at wileyonlinelibrary.com]

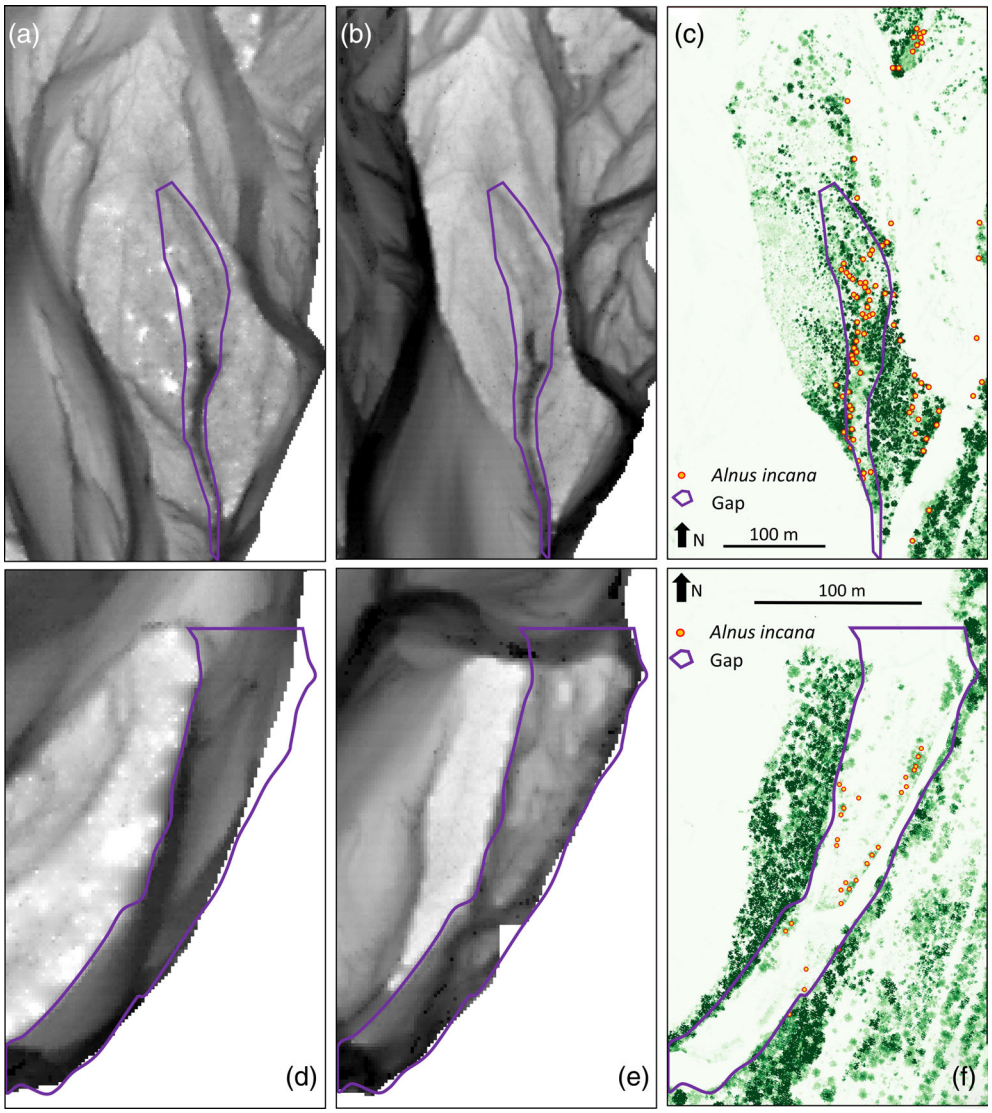


FIGURE 4 Gap 1 (a–c) and Gap 2 (d–f), showing the 2005 detrended DEM (a,d), 2013 detrended DEM (b,e) and 2013 distribution and relative height of the vegetation cover (estimated from lidar data, vegetation height ranges from 0 m [white] to >15 m [darkest green]) and positions of alder individuals surveyed in 2019 (Gap 1) and 2018 (Gap 2) (c,f) [Colour figure can be viewed at wileyonlinelibrary.com]

3.2.1 | Gap 1

The channel occupying this narrowest gap is seen between unvegetated bars in 1986 (Figure 2). By 1993, widespread patchy vegetation encroaches the downstream part with some lines of young shrubs in the upstream parts and numerous pioneer islands across the bar surface upstream of the gap. By 1997, the gap encloses a continuous linear area of bare sediment, presumably created during the 1996 floods. In the northern part, an elongated vegetated area within the western side has absorbed the lines of young shrubs observed in 1993 and the eastern part of the gap displays several new parallel lines of young shrubs. By 2003, the upstream part is obscured by continuous vegetation and the downstream part has extended to the southern tip of the island. An area of bare sediment can still be seen within the central part of the gap in the 2005 image and the entire gap is completely concealed by vegetation in all subsequent images (not shown). Throughout this time sequence, pioneer islands are seen on open areas of sediment, particularly in the northern (upstream) part of the mapped area, whereas lines of young shrubs generally develop in the central part of the mapped area, particularly within evolving gaps between established vegetated areas. The 2005 and 2013 DEMs (Figure 4a,b) show the large bar on which the main mapped island has developed with a bar head to the north where most pioneer islands developed over the image sequence. Three minor channels in the northern part of the gap join to form a single channel within the central and southern parts (Figure 4a,b). Virtually all of the mapped *A. incana* individuals taller than 4 m in 2019 (Figure 4c) are located along the edge of the channel through Gap 1 and along a smaller channel crossing the eastern part of the island on the 2005 DEM.

3.2.2 | Gap 2

Gap 2 was enlarged by the 2000 flood and disturbed by another significant flood peak in November 2002 (Figure 1b) so that in 2003 (Figure 3), it is only occupied by bare bars and braid channels with a few deposited trees, three of which are aligned towards the head of a bar within the upstream half of the gap. In 2005, there are three

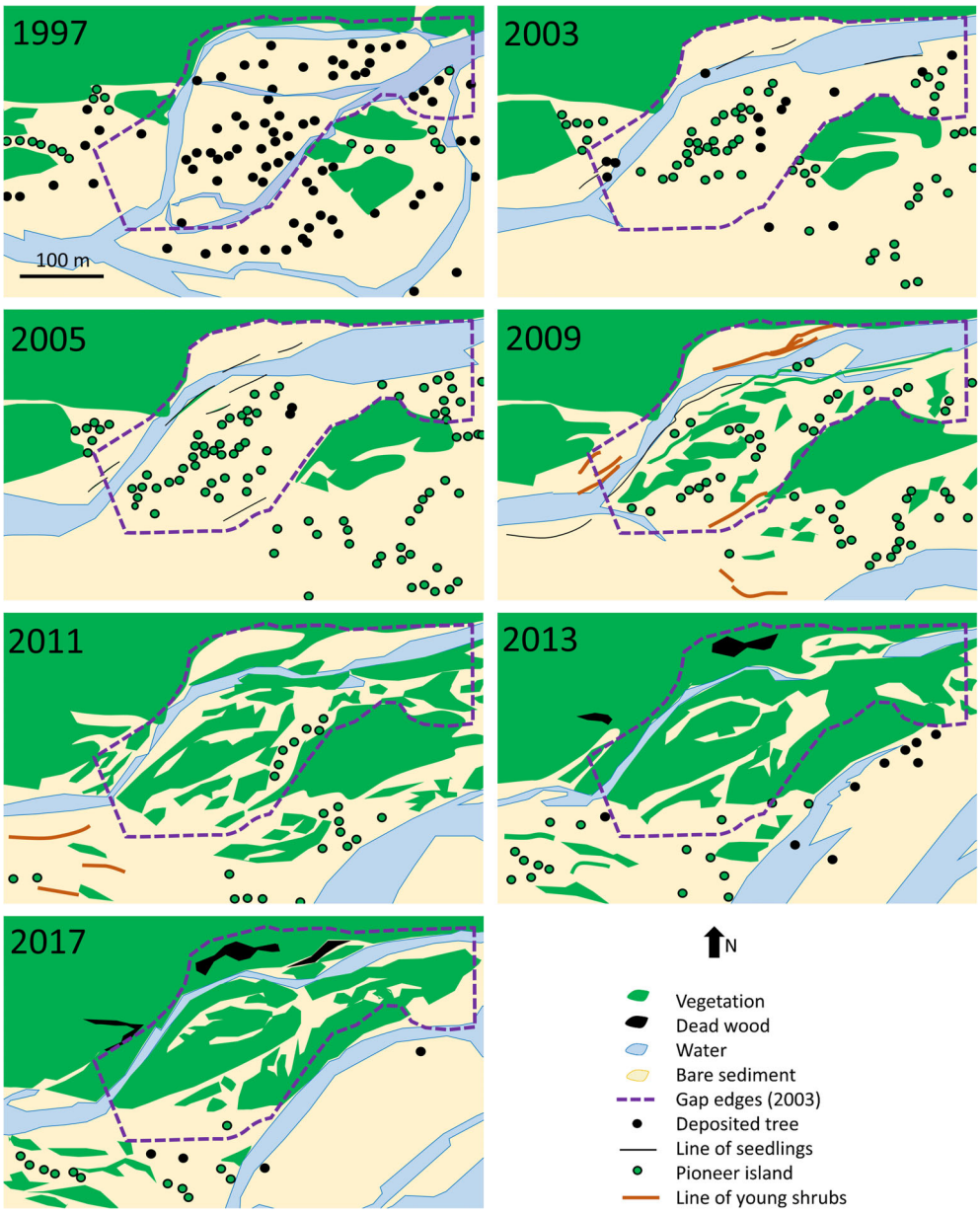


FIGURE 5 Maps of the distribution of cover types and vegetation features in and around Gap 3 interpreted from aerial images captured in 1997, 2003, 2005, 2009, 2011, 2013 and 2017 (flow is from east-north-east to west-south-west) [Colour figure can be viewed at wileyonlinelibrary.com]

pioneer islands at the upstream end of the gap, two at the same location as deposited trees in 2003. These two deposited trees/pioneer islands persist within the vegetation cover until the 2017 image. A nearby pioneer island, observed to the north east in 2005, also persists within the extending vegetation cover until at least 2013. In 2009, two new pioneer islands are observed along the western side of the upstream bar and lines of seedlings are seen forming downstream from the two original pioneer islands, along the eastern and western margins of the upstream bar and on the head of the downstream bar within the gap. In 2011, the 2009 lines of seedlings are lines of young shrubs; additional shrub lines are evident along the eastern edge of the downstream bar and around the upstream bar tail. New pioneer islands are present on the upstream bar and several pioneer islands and lines of seedlings/shrubs from 2009 are incorporated into vegetated areas along the western side of the gap. By 2013, all of the pioneer islands and lines of shrubs present in 2011 are incorporated into elongated vegetated areas. By 2017, vegetation cover has expanded, providing a complex structure that has trapped floating wood, retaining enormous rafts and smaller patchy accumulations of wood. Over the time sequence, the upstream end of the gap has been the predominant area for deposition of large uprooted trees which often develop into pioneer islands, whereas the central and downstream areas have mainly supported development of lines of seedlings and other small propagules which, if they survive, develop into lines of shrubs. The 2005 DEM (Figure 4d) shows two streamlined bars in the upstream and downstream parts of the gap, which by 2013 (Figure 4e) display distinct elevated patches on their surfaces. The upstream bar shows elevated areas around the three early pioneer islands at the bar head and elongated elevated areas along the central, western edge and the central to downstream part of the eastern bar

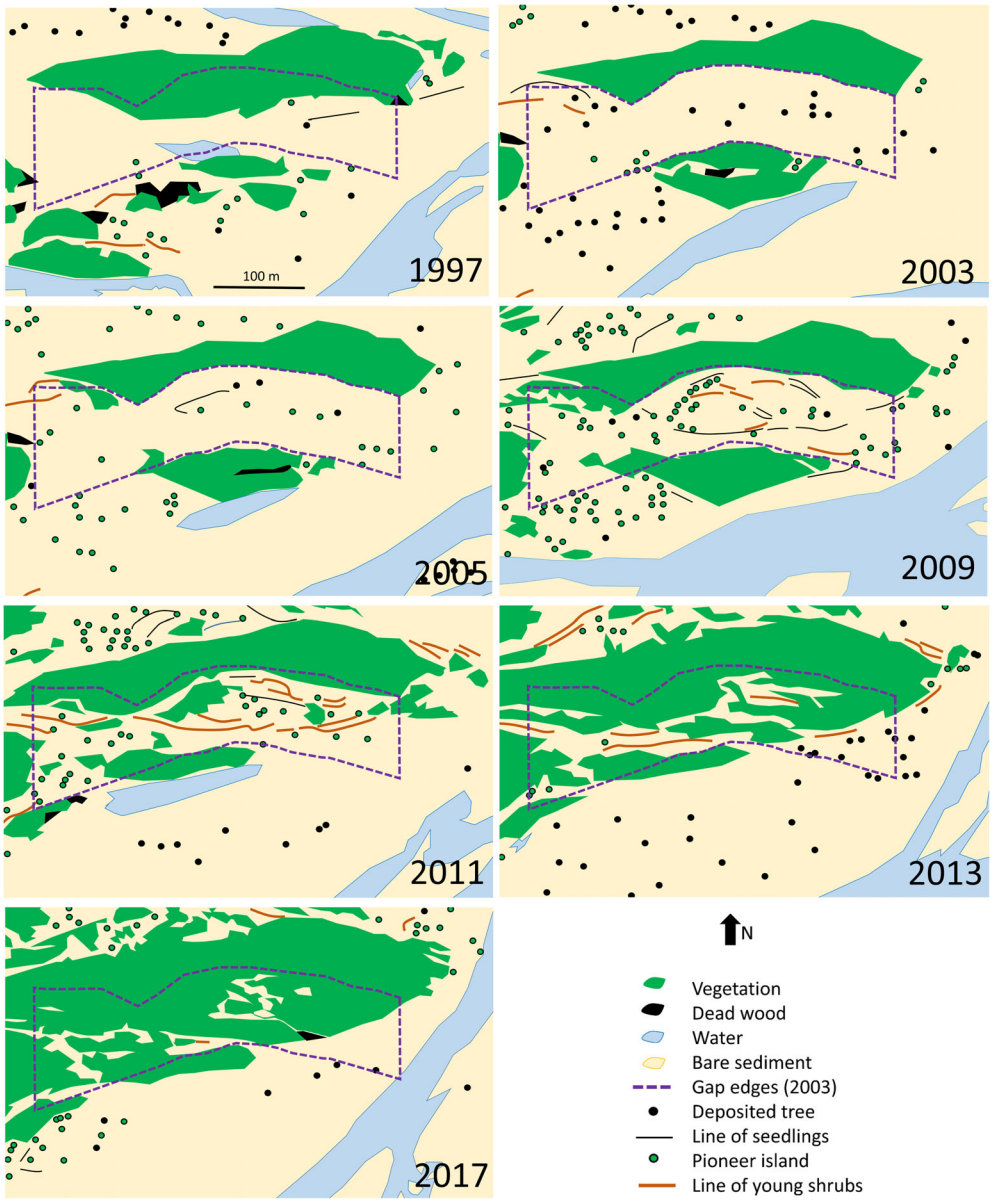


FIGURE 6 Maps of the distribution of cover types and vegetation features in and around Gap 4 interpreted from aerial images captured in 1997, 2003, 2005, 2009, 2011, 2013 and 2017 (flow is from east to west) [Colour figure can be viewed at wileyonlinelibrary.com]

edge. *A. incana* individuals in this gap could not be mapped in 2019, but mapping in 2018 revealed near-continuous lines of *A. incana* on the surfaces of these elongated features. A subset of these trees, individually mapped and measured in 2018, are indicated in Figure 4f.

3.2.3 | Gap 3

The outer limits of Gap 3 (Figures 5, 2003 image) were established following the 2000 flood, which eroded extensive floodplain edges along the north side of the gap (compare 1997 image). Following the 1996 floods (Figure 5), numerous trees were deposited across unvegetated bar surfaces. By 2003, numerous pioneer islands are present on bar surfaces and deposited trees, possibly from the 2000 flood, contribute to more widespread pioneer islands in 2005. Also in 2005, several parallel lines of seedlings are evident, some of which are observable in 2003 and were probably initiated following the 2000 flood, whereas some probably reflect flow paths during the 2004 flood. By 2009, many of the 2005 pioneer islands in the central part of the gap have coalesced to form larger vegetated areas. Quasi-parallel, linear vegetation features, particularly bordering the braid channel to the north of the main bar, include lines of seedlings, young shrubs and more mature vegetation, were probably initiated by different flood events. The 2011, 2013 and 2017 images show progressive vegetation encroachment across the gap as pioneer islands and lines of shrubs are absorbed into elongated vegetated areas running approximately parallel to the adjacent channels. Beyond the gap, deposited trees and pioneer islands are observed in all the three later images but few lines of seedlings or young shrubs are evident. The 2005 and 2013 DEMs (Figure 7a,b) display elongated ridges on a large central bar, all aligned approximately parallel to the channels on either side of the bar. All alder trees mapped in 2019 are positioned in lines along the edges of

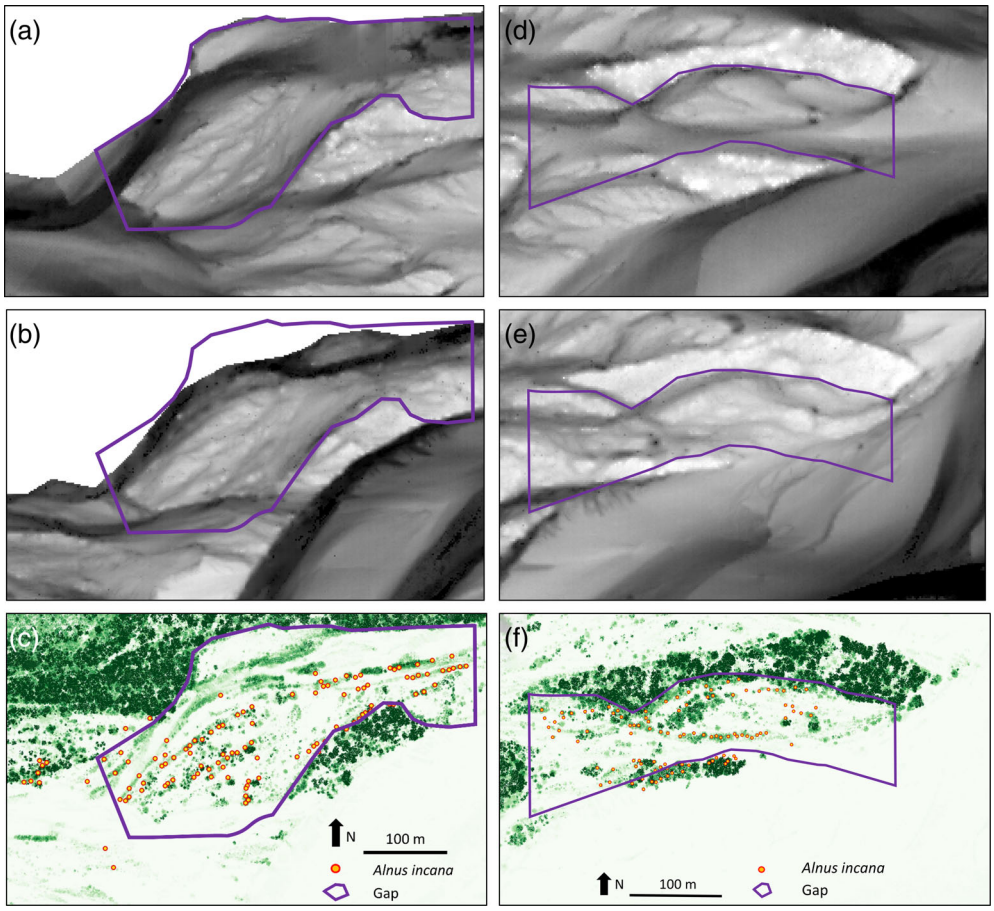


FIGURE 7 Gap 3 (a–c) and Gap 4 (d–f), showing the 2005 detrended DEM (a,d), 2013 detrended DEM (b,e) and 2013 distribution and relative height of the vegetation cover (estimated from lidar data, vegetation height ranges from 0 m [white] to >15 m [darkest green]) and positions of alder individuals surveyed in 2019 (c,f) [Colour figure can be viewed at wileyonlinelibrary.com]

the tallest vegetated areas and elongated ridges, particularly on the central and southern parts of the main bar (Figure 7c).

3.2.4 | Gap 4

Like Gaps 2 and 3, the outer limits of Gap 4 were established following the 2000 flood (Figure 6, 2003 image), which trimmed the edge of the large island on the northern side of the gap. In 2003 the gap contained a number of deposited trees, probably from the 2000 flood, but was unvegetated apart from a few pioneer islands and some lines of seedlings and young shrubs confined towards the downstream (western) end of the gap. By 2005, the number of pioneer islands had increased and mainly appears to reflect sprouting of deposited trees observed in 2003. There is little evidence of the effects of the 2004 flood apart from a line of seedlings towards the centre of the gap, the addition of a few deposited trees and the removal of some previously deposited trees. By 2009, pioneer islands and lines of seedlings and young shrubs follow the edges of the central bar and some dry channels. A line of pioneer islands at the centre of the gap may represent shrubs that have grown from patches of seeds and small vegetated fragments along a disrupted flood trash line. By 2011, vegetated areas have developed around many of the 2009 pioneer islands and lines of young shrubs broadly follow 2005 lines of seedlings and shrubs. Through 2013–2017, all of these vegetated features are absorbed into expanding areas of vegetation. Towards the main channel and to the south of the gap, deposited trees and pioneer islands appear and disappear across areas of bare sediments but few linear vegetated features are observed. The 2005 DEM (Figure 7d) reveals a large streamlined bar bordered by channels in the central part of the gap, with some smaller channels crossing the bar. The edges of these features correspond to the lines of seedlings and young shrubs observed in the aerial images. The 2013 DEM (Figure 7e) shows a similar spatial pattern of bars and channels but with some more elevated areas across the central bar and to the west (downstream) and east (upstream) within the gap, which correspond with the 2013 vegetated areas (Figure 7f). Alder trees mapped in 2019 (Figure 7f) are aligned along the edges of these linear features, particularly along the northern and southern sides of the central bar and in the downstream part of the gap, and along the edges of the island on the southern side of the gap.

3.3 | Tracking the heights of *A. incana* individuals through 2005, 2010 and 2013

As previously noted, the alder trees mapped in 2019 (2018 in Gap 2) almost entirely grow in lines, are associated with linear topographic features, and very frequently correspond to lines of seedlings/young shrubs observed on the aerial images. The bar graph in Figure 8 shows the average height of these alder trees for selected subareas of Gaps

1, 2, 3 and 4 and their immediate surroundings in 2005, 2010 and 2103, estimated from lidar data. Maps of the vegetation distribution and the locations of the surveyed alders in and around Gaps 1, 2, 3 and 4 are presented in Figure 8 in relation to black ellipses bounding the sub areas depicted in the bar graph.

Based on an average annual growth rate of 0.6 m (Bertoldi & Gurnell, 2020), the average heights of alder trees presented in the bar graph (Figure 8) suggest that those in the central and downstream part of Gap 1 (Figure 8, Area 1A) and in the small gap to the east (Figure 8, Area 1B) pre-date the 1996 floods, whereas those in the upstream part (Figure 8, Area 1C) date back to around the time of the 1996 floods. The alder trees in Gap 2 date back to the 2004 flood. In Gap 3, the oldest alder trees appear to date back to the 1996 floods and are found along the edge of the island on the southern side of the gap (Figure 8, Area 3A) whose edges were not trimmed by the 2000 flood. The alders in Areas 3B and 3C date to the 2000 flood, or possibly the 2004 flood in area 3C. In Gap 4, the alder trees around the island on the south side of the gap (Figure 8, Area 4A), an area which was not eroded by the 2000 flood, date back to 1996. The alders in Areas 4B, 4C and 4D (Figure 8) are positioned in the downstream (4B) part of the gap and on the north (4C) and south edges (4D) of the bar in the centre of the gap. These three areas show progressively shorter trees and appear to date to the floods of 2000 (4B) and 2004 (4C and 4D). All of these dates confirm the previous interpretations of vegetation development (Section 3.2), particularly in relation to lines of seedlings and young shrubs.

4 | DISCUSSION

4.1 | A sequence of vegetation and landform development in and around gaps

Although riparian vegetation encroachment in braided rivers is a highly complex, multi-scale process (Belletti, Dufour, & Piégay, 2014; Räpple, Piégay, Stella, & Mercier, 2017), based on our detailed observations (Sections 3.2 and 3.3), the four investigated gaps showed many common evolutionary features, tracked from an unvegetated state following a large flood to a state where they support extensive riparian woodland superimposed upon aggraded river bed landforms, which we interpret below in relation to our three working hypotheses (see Section 1).

Deposited trees/pioneer islands are observed throughout all of the gaps, across bars beyond the gaps, and at all stages in the evolution of gaps from an unvegetated to a fully vegetated state. They are the key element of Pathway (3) of the island model (Figure 9a). In almost all cases, the deposited trees that sprout, root-anchor themselves on bar surfaces, and then interact with transported sediments to create

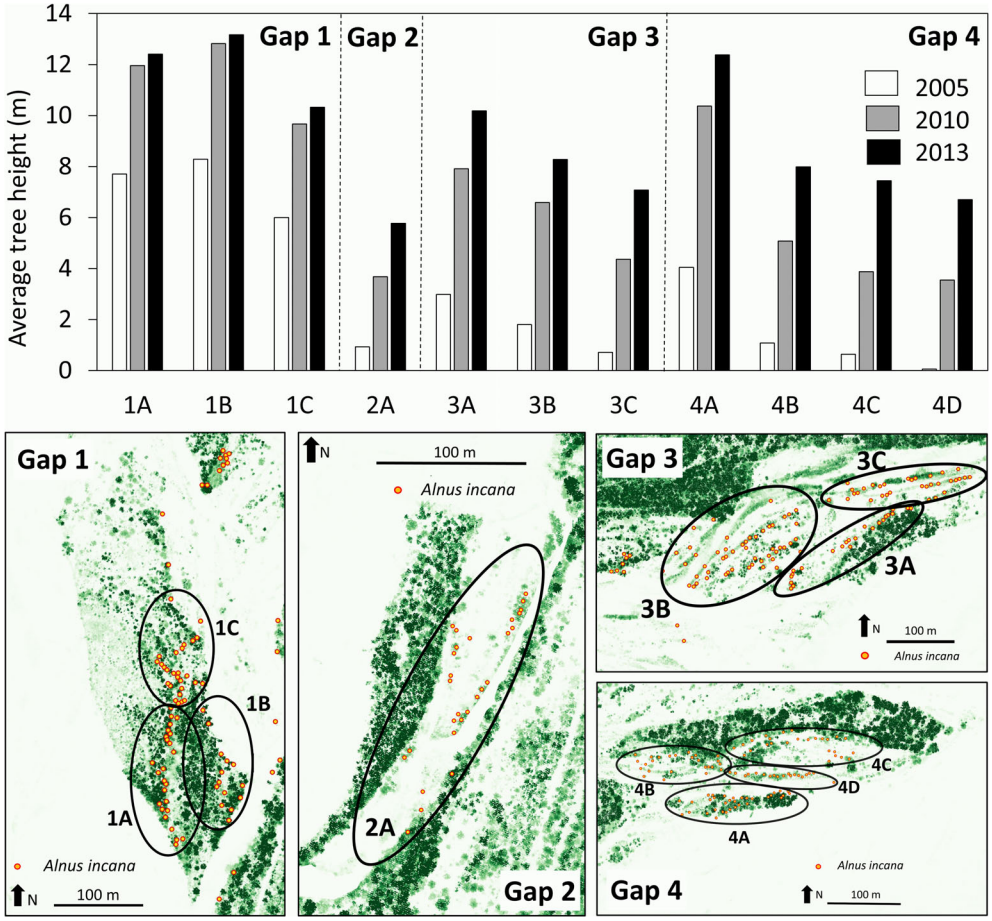


FIGURE 8 Above—Bar graph of the average height of field-surveyed alder trees in 2005, 2010 and 2013 (estimated from lidar data) within subareas in and around Gaps 1, 2, 3 and 4. Below—Maps of the distribution and relative height of the vegetation cover in 2013 (vegetation height ranges from 0 m [white] to >15 m [darkest green]); the positions of alder individuals surveyed in and around each gap in 2018 and 2019; and the subareas in and around each gap for which average alder tree heights were estimated from the 2005, 2010 and 2013 lidar surveys [Colour figure can be viewed at wileyonlinelibrary.com]

pioneer islands are *P. nigra*. Occasionally other Salicaceae species sprout and drive pioneer island development, but Pathway (3) is extremely rarely related to *A. incana* within the study reach.

Lines of seedlings and young shrubs are rarely observed and, when present, rarely survive for long in the earliest stages of gap evolution or in the more exposed areas outside of the gaps. Lines appear to form preferentially in the central and downstream parts of gaps. This indicates that lines of seedlings form in the study reach where there is some shelter provided by a gap and/or (pioneer) islands, supporting hypothesis (a) that a reduction in exposure to flood disturbance enhances the relative importance of sexual reproduction in the initiation of vegetated areas. The lines appear to correspond to flow "trash lines" along channel and bar margins and sometimes in the lee of deposited trees and pioneer islands. They are an expression of Pathway (2) of the island model (Figure 9a), since trash lines are usually composed of dead wood, other dead organic material and seeds, but they may also incorporate viable woody fragments. The lines are most likely to develop from seedlings that benefit from macro-shelter by the vegetated sides of the gap and within-gap pioneer islands and also micro-shelter from dead and living-sprouting wood within the trash line. These suppositions are supported by the following facts: *A. incana* individuals are almost completely confined to these lines; this species rarely reproduces vegetatively in its early years; unlike species of the Salicaceae family, *A. incana* produces a seed bank and so has an extended time period (possibly more than a year, Thompson et al., 1997) within which its seeds may germinate.

Nevertheless, trash lines may also promote vegetative reproduction from small as well as large woody fragments. While *A. incana* has occasionally been observed to produce stump sprouts from deposited trees in the study reach, field experiments on the Tagliamento with smaller *A. incana* cuttings have universally failed and sprouts have rarely been observed on roots exposed by erosion (authors' personal observations). Furthermore, laboratory experiments employing varied soil moisture regimes and sediment calibres have shown extremely poor survival rates for *A. incana* cuttings but high survival of two Salicaceae species, *P. nigra* and *Salix eleagnos* (Francis et al., 2005). Therefore, any asexual recruitment pathway is likely to be confined to Salicaceae species. Furthermore, as pioneer islands and lines of shrubs develop, areas of sheltered but open, relatively fine, moisture-retentive sediments may accumulate along the sides and lee of these vegetated landforms that could support recruitment from spring-dispersed Salicaceae seeds. Corenblit et al. (2016) observed on the Garonne River, France, how a single Salicaceae species, *P. nigra*, engineered bar surfaces and supported their aggradation, lateral

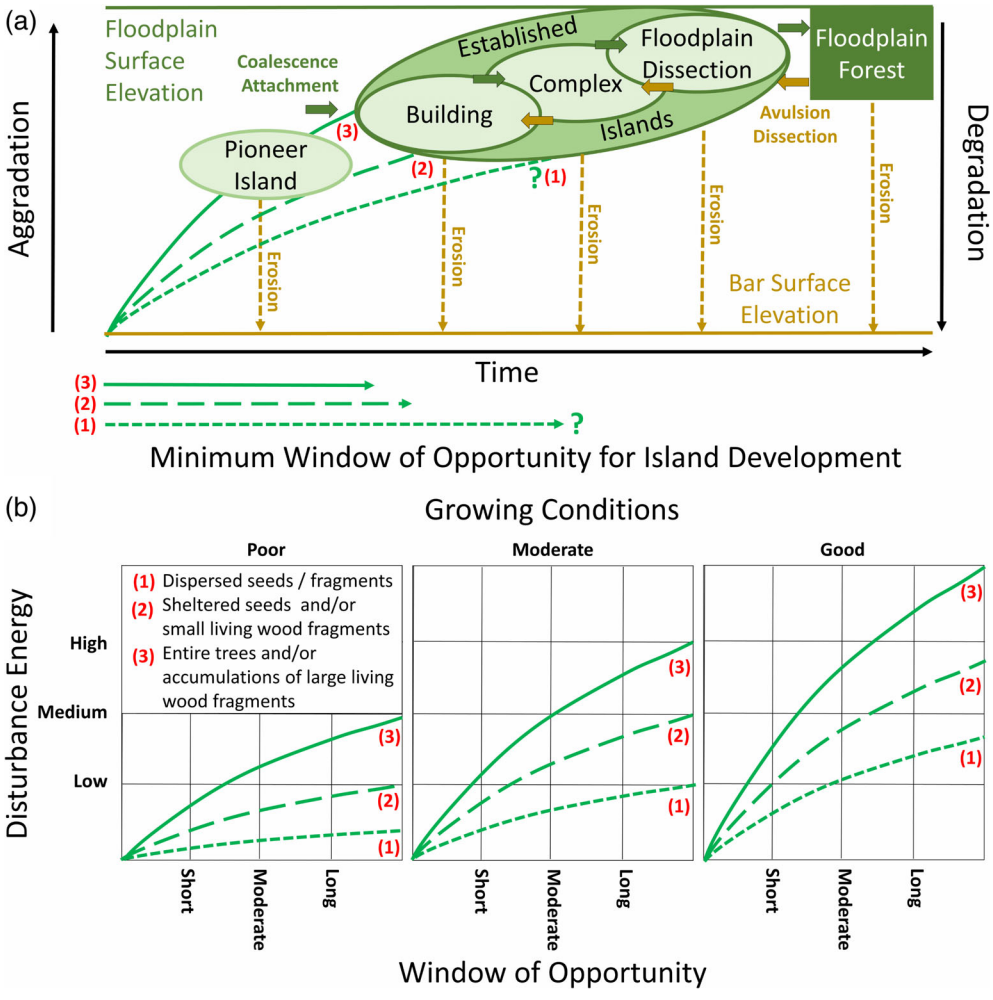


FIGURE 9 (a) The conceptual model of island development proposed by Gurnell et al. (2001, 2005). Three different vegetation development pathways (1, 2 3) are associated with progressive aggradation and reinforcement of vegetated landforms and, potentially, the development of established islands and new areas of floodplain. The likely success of each pathway in driving island development depends upon the length of the window of opportunity in relation to the growth performance of trees whose growth is initiated by three different types and sizes of propagule. (b) Idealized growth curves displayed by three different vegetation development pathways according to the impact of local growing conditions on tree growth performance, the length of the window of opportunity between floods, and the local disturbance energy/shear stress imposed by floods at the end of the window of opportunity [Colour figure can be viewed at wileyonlinelibrary.com]

and downstream extension as chronological sequences of stands grew in the shelter of established stands. On the Allier River, France, Tinscert, Egger, Wendelgaß, Heinze, and Rood (2020) found that the most genetically diverse stands of *P. nigra* were found on the least disturbed sites, supporting our proposal that where this species develops on bare, highly disturbed sites, it reflects a pathway driven by vegetative reproduction, although recruitment from seeds may occur in less-disturbed, sheltered locations. This is also supported by Barsoum (2002), who observed that early stage recruitment of *P. nigra* along the Drôme River, France, was predominantly from seed, but poor survival over time in response to flood disturbances induced a shift towards vegetative regeneration.

Hortobágyi, Corenblit, Steiger, and Peiry (2018) highlighted the engineering roles of different Salicaceae species on the Allier River, where *P. nigra* acts as the main engineer species at the bar scale but two other Salicaceae species, *Salix purpurea* and *Salix alba* with slightly different traits, respectively, colonized and physically engineered the bar sides (coping with the most exposed positions) and tail (benefitting from the most sheltered locations). Here, we have shown the importance of even stronger contrasts in the traits displayed by two riparian trees species drawn from different families for the physical engineering of islands and floodplain edges on the highly disturbed Tagliamento. This exemplifies hypothesis (b) that "vegetated area initiation and development displays distinctive spatio-temporal patterns reflecting traits of the colonizing woody species." Not only is initial colonization by *P. nigra* dominated by vegetative reproduction and the development of pioneer islands, but the presence of pioneer islands, particularly at the head of gaps, produces sufficient shelter for seedlings to survive. Furthermore, because of the predominance of autumn floods, initial colonization of open sites requires seeds that are viable in the autumn, precluding those of Salicaceae species but supporting colonization by *A. incana*. Thus seedling colonization of bare areas of sediment on the Tagliamento is dependent on some shelter from flood disturbances, which is often facilitated by the presence of *P. nigra*-driven pioneer islands, but as lines of seedlings and shrubs dominated by *A. incana* grow, Bertoldi and Gurnell (2020) show that they interact with transported sediments to perform a physical engineering role, building linear landforms that often border developing islands and maintain channel edges. In the case of *A. incana*, sheltered areas not only provide some protection for the developing seedlings, but also the relatively finer, free-draining but relatively moisture-retentive substrates that experiments suggest the species prefers (Hughes et al., 1997). Thus *A. incana* and *P. nigra* adopt central positions in two different but complementary Pathways ((2) and (3)) that drive island development within the study reach.

If they survive, vegetated gaps may have several possible fates. Narrow gaps (e.g., Gap 1) may continue to support relatively gentle flows of water during floods and isolated ponds during low flows, reflecting their small size, high boundary roughness and strong bank reinforcement by tree roots. Bank reinforcement is likely to be particularly effective where the channels are bordered by *A. incana*, because this species is frequently observed to spread its roots across the surface of bank faces in the study reach. Wider gaps tend to be bordered by channels with one or more central bars that aggrade to form islands. In the second widest gap (Gap 2) one of these channels had become dominant by 2018 (Figure 10), with the second channel

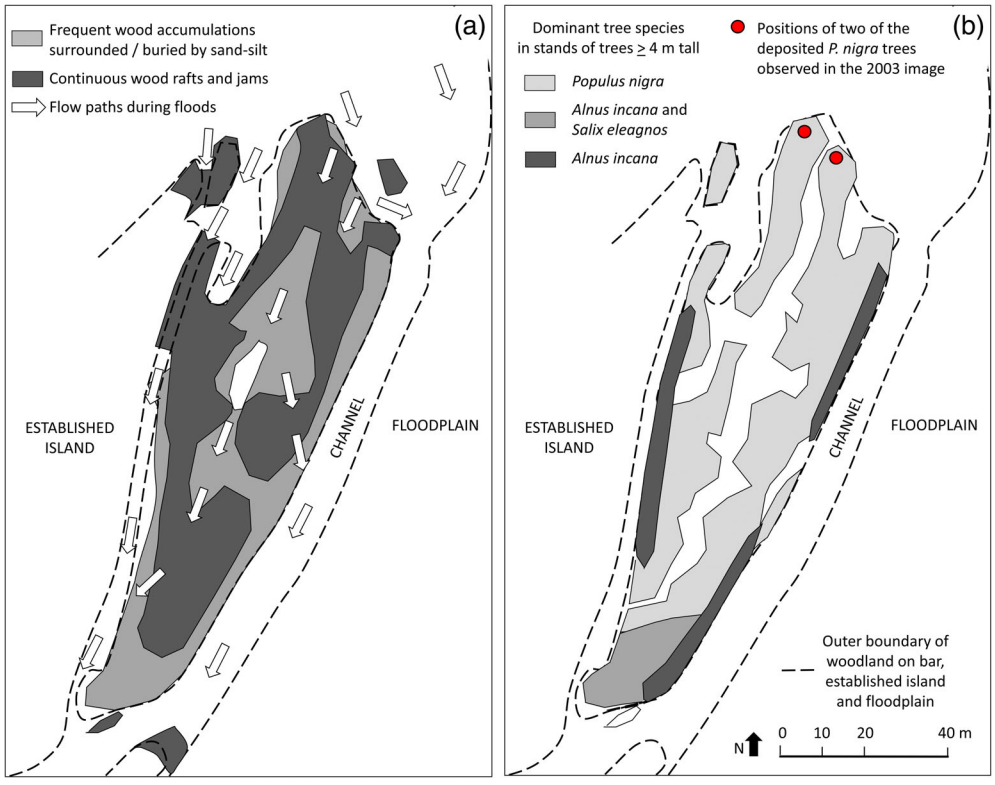


FIGURE 10 The upstream (northern) part of Gap 2, surveyed in 2018, showing a large bar occupying the gap with channels separating it from the floodplain in the east and an established island in the west (flow direction is from north to south): (a) The spatial extent of continuous and discontinuous wood rafts, jams and accumulations and the direction of flow paths that would be occupied during high river flows. (b) The spatial extent of vegetated areas, the dominant tree species in each area and the position of the two surviving *P. nigra* individuals seen as deposited trees in the 2003 image and pioneer islands in the 2005 image [Colour figure can be viewed at wileyonlinelibrary.com]

blocked at its upstream end by a large wood jam (Figure 10a). If vegetation and island development had continued beyond 2018, it is likely that the island that had developed within the gap would have attached to the established island along its western margin, forming a greatly enlarged and "complex" established island (Figure 9a). The widest gaps (Gaps 3 and 4), although only supporting channel flow during floods, maintained distinct channels throughout their evolutionary sequence along both gap edges (Figure 7), suggesting that they may be sufficiently wide to support the development of new established islands (Figure 9a) within the gap. However, it is possible that the evolving islands might eventually attach at one or both sides and that the channels might simply fill or be maintained as persistent flood channels similar to that displayed by Gap 1. Overall these variations in the patterns of vegetation and related landform development within the four gaps reflect the survival and growth of woody species under the influence of flood disturbance energy, windows of opportunity between disturbances and local growing conditions (shelter, substrate moisture retention), supporting hypothesis (c).

Mapping of Gap 2 in 2018 (Figure 10), illustrates the key general features described above, including the importance of pioneer islands at the gap head (red dots, Figure 10b) which protect sediments accumulating in their lee to form linear ridges. Once shelter from pioneer islands is combined with shelter along gap and bar margins, viable deposited seeds or vegetative fragments contained within linear trash lines can germinate or sprout. Because of the extended viability of its seeds, the germinating species is most likely to be *A. incana*, which builds linear ridges as it grows that protect the sides of the channels, bars and (pioneer) islands where the trash lines were deposited. While the head and central part of the island within Gap 2 is dominated by *P. nigra*, the edges and tail are dominated by *A. incana*, with some *Salix eleagnos* (Figure 10a). The developing vegetation cover in this modest-sized gap has also trapped enormous quantities of dead wood (Figure 10a) which has been retained from flood flows across and around the developing vegetation cover as local accumulations and vast rafts of wood. These are clearly visible in the 2017 aerial images (Figure 3) and may further support vegetation development Pathways (2) and (3) in colonizing areas of bare sediment (flow pathways) across the building island surface. There is little evidence of vegetation development Pathway (1), although young alder growing around the edges of the alder lines is most likely from local seed dispersal, and some young *P. nigra* and other Salicaceae species may have developed from seeds deposited on bare sediments in open but sheltered locations in the lee of developing vegetation patches.

4.2 | An extended conceptual model of island development

The original conceptual model of island development, inspired by observations along the Tagliamento River (Gurnell et al., 2001, 2005; Figure 9a), emphasized that vegetation development Pathway (1) is unlikely to be successful, mainly because it requires longer windows of opportunity than are typically available on this river. However, Pathway (1) may support vegetation development in areas sheltered by vegetation patches created by the other two pathways. Pathway (3) is observed to be the most successful. It drives island development in the middle and lower reaches of the river where *P. nigra* is the dominant riparian tree species. Pathway (2) is observed quite widely in the river's headwaters, where the dominant riparian tree species are *S. eleagnos* and *A. incana* (Karrenberg et al., 2003) and large dead wood accumulations are available to shelter seedlings. Pathway (2) complements Pathway (3) in the middle reaches (Gurnell et al., 2000, 2001). In the lower reaches, Pathway (2) may also be active in the tail of scroll bars (elongated pioneer islands that develop around lines of sprouting deposited trees—Pathway (3)) on the inside of meander bends (Zen, Gurnell, Zolezzi, & Surian, 2017; Zen, Zolezzi, Toffolon, & Gurnell, 2016).

Gurnell and Petts (2006) extended the island development model by considering the opposing effects of unit stream power and groundwater depth in widening and narrowing reaches of the Tagliamento. They suggested that in the widest reaches, deeper groundwater levels might reduce plant growth performance to such an extent that islands would not develop, even though the unit stream power associated with any particular flood event would be much smaller than in narrower reaches. They also suggested that in very narrow reaches, higher tree growth rates promoted by groundwater upwelling and near-surface water tables would be insufficient to resist the increase in flood unit stream power and thus would prevent island development. They proposed that island development would be most extensive in reaches of intermediate width, where intermediate rates of tree growth would be sufficient to support island development under intermediate levels of unit stream power. This reach-based approach to framing the likely success of river physical engineering by plants was upscaled to consider the extent and nature of river bed engineering by riparian and aquatic plants across rivers of widely contrasting energy and planform styles (Gurnell et al., 2012).

Figure 9b is concerned with river bed engineering by riparian trees and conceptualizes interactions among tree growth performance along Pathways (1), (2) and (3) according to three controlling factors that operate across multiple time and space scales. The first factor is growing conditions. This control operates at all spatial scales from biogeographical region to river catchment to river reach to patches within reaches. Although many factors influence growing conditions for riparian trees, moisture availability is crucial and is dependent upon substrate calibre (water retentiveness), river water surface and alluvial groundwater levels. Different vegetation development Curves (1), (2) and (3) can be conceptualized for a single tree species under "poor," "moderate" and "good" growing conditions (the three graphs shown in Figure 9b). How far vegetation development can progress along each curve depends upon the two remaining controlling factors. The second control is the window of opportunity that is available following germination or initial sprouting of vegetative propagules (horizontal axis on all graphs, Figure 9b). This controlling factor is entirely time dependent, remembering that for species that do not support a seedbank, the start of the curve is the season of seed production, whereas for other sexual or asexual propagules, it can be any time in

the growing season. The third controlling factor is flood disturbance. In relation to flood disturbance, the development curves can be interpreted as vegetation resistance, since any disturbance that plots higher than a given curve would remove vegetation following that development curve. The frequency and magnitude of floods varies through time, generating extreme flow events of widely varying total power or energy. Total stream power is distributed across the width of the flow, resulting in longitudinal reach-scale variations in unit stream power according to flow width for any single value of total stream power. Furthermore, within a reach, stream power is distributed unevenly according to three-dimensional patterns of water depth and shelter, so that disturbance energy (vertical axes, Figure 9b), the bed shear stresses that it exerts and the resulting severity of sediment erosion and deposition processes can vary across all spatial scales. This has the potential for plants following vegetation growth Pathway (1) to survive locally and Pathway (2) to survive more widely in "seedling safe zones" (Polzin & Rood, 2006) within reaches where only those following Pathway (3) may be capable of resisting removal in the most exposed sites.

The above-described multi-scale approach to considering the success of the different vegetation development pathways, can be interpreted by referring to three scenarios. In wide unvegetated rivers or wide gaps in the largest rivers subject to frequent, high energy disturbances, only Pathway (3) can lead to island development where growing conditions are also good and a sufficiently long window of opportunity occurs. Thus, Pathway (3) is the only pathway that builds enough plant resistance for vegetation to persist under high disturbance energy (horizontal lines) and this only occurs under good growth conditions when the window of opportunity (vertical lines) is greater than moderate (right graph, Figure 9b). Under these restricted circumstances, vegetation development Pathway (3) can lead to pioneer island and possibly established island development. In contrast, in rivers where disturbing flows are of relatively low energy (lowest horizontal lines in all graphs, Figure 9b), all pathways can lead to successful vegetation development under good growing conditions, although Pathway (1) requires at least a moderate window of opportunity. Under moderate growing conditions, Pathway (1) is unlikely to be successful, but Pathway (2) may succeed in driving island—floodplain development if the window of opportunity is moderate, and Pathway (3) is likely to be successful regardless of the length of the window of opportunity. Between these examples, an infinite number of combinations are feasible, but we can consider the study reach of the Tagliamento as an illustration and investigate the fate of two engineer tree species. As the primary engineer, *P. nigra* initially colonizes exposed sites, so it suffers high energy disturbances (highest disturbance line) and thus may only survive by following Pathway (3) to build pioneer islands that aggrade into established building islands (right graph, Figure 9b). However, if deposited by a sufficiently large flood, trees following Pathway (3) will be floated into relatively elevated positions, and if the window of opportunity is sufficiently long, they may induce aggradation so that the developing pioneer island may only suffer medium disturbance from a later high magnitude event and may continue its trajectory towards island development (middle graph). Thus, as deposited *P. nigra* individuals grow, they can reduce the intensity of their exposure to disturbance from a flood event of a given size and they may also induce areas of reduced flood disturbance energy for propagules of the same species following other growth pathways. This can be extended to other species that may preferentially follow other development pathways. *A. incana* tends to follow Pathways (1) and (2) because of its stronger dependence on sexual reproduction in its early years. In the study reach, Pathway (1) is unlikely to be successful, because even in sheltered, elevated positions, where flood energy may be reduced locally to medium levels, good growing conditions and a long window of opportunity are needed to resist even low disturbances (right graph). This explains why this pathway is unlikely to contribute to island development unless it develops from trash lines that are already sheltered within gaps and/or benefit from shelter by pioneer and established islands and within embayments in floodplain edges. However, the species may successfully grow in trash lines under moderate growing conditions in lower energy rivers (middle graph) where disturbance energy is generally lower, particularly if the window of opportunity is sufficiently long.

Of course, the words "poor," "moderate," "high" applied to growing conditions; "short," "moderate," "long" applied to windows of opportunity, and "low," "medium" and "high" applied to disturbance energy are all qualitative and can be conceptualized across different time and space scales and in relation to different riparian species. Figure 9b provides a significant advance of the island model because, for the first time, it allows more than one tree species drawn from different families and possessing different life history traits to be incorporated, emphasizing that different species may engineer river landforms in different and complementary ways. Previous research has explored and modelled how riparian plant species with different life history traits respond to environmental conditions and their changes (e.g., Bornette et al., 2008; McCoy-Sulentic et al., 2017; Merritt, Scott, LeRoy Poff, Auble, & Lytle, 2010; Stromberg & Merritt, 2016) and has started to consider how plant traits may be relevant to fluvial geomorphology (e.g., Hortobágyi et al., 2018; O'Hare, Mountford, Maroto, & Gunn, 2016; Tabacchi et al., 2019). The extended conceptual model of island development builds on such ideas by considering their species-specific and complementary consequences for river landform development.

5 | CONCLUSIONS

In conclusion, our observations of physical ecosystem engineering by *P. nigra* and *A. incana* within the study reach of the Tagliamento, emphasizes that on this high energy river, patches of vegetation that survive within the braid plain are mainly initiated by vegetative reproduction from large propagules (usually whole uprooted trees). Because the dominant species, *P. nigra*, reproduces freely vegetatively, this is the key engineering species to sprout and build pioneer islands on the braid bar surfaces (vegetation development Pathway (3)), although other Salicaceae species may also initiate pioneer islands. Furthermore,

even when extended windows of opportunity arise, Salicaceae species are unlikely to initiate new vegetated patches from seeds (Pathways (1) and (2)) because their seeds are released in Spring; they have a short period of viability; and the largest floods on the Tagliamento occur in Autumn (when there are no viable seeds to disperse and when any young seedlings of the year are too small to survive). In contrast, *A. incana* does not reproduce readily by vegetative means, particularly when trees are fairly young (i.e., within the age range constrained by island turnover on the Tagliamento, Zanoni, Gurnell, Drake, & Surian, 2008). Therefore, *A. incana* is very unlikely to drive pioneer island development (Pathway (3)), but this species releases seeds in Autumn that have an extended period of viability and so may benefit from dispersal by floods to suitable sites to initiate Pathways (1) and (2). Even so, seedlings are unlikely to survive in the high energy environment of the Tagliamento unless they receive some macro- (potentially Pathway (1)) or micro- (Pathway (2)) shelter from flood flows. On the study reach, *A. incana* mainly benefits from macro-scale shelter downstream from pioneer islands and in gaps between established islands. These (lightly sheltered) locations may also offer slightly finer, more moisture-retentive, open sites to support *A. incana*, germination and growth. Thus, landforms built by *P. nigra* on the surfaces of gravel bars facilitate nearby colonization by *A. incana*. Because *A. incana*, in turn, initiates distinct linear vegetated patches that trap sediments and aggrade, both species act as physical ecosystem engineers, building landforms that may or may not become joined to one another in the early development stages. The two species act as complementary physical ecosystem engineers, building separate and combined landforms that reflect their different traits and growing environmental requirements.

Although tree species, hydrological and geomorphological conditions may differ within and between other temperate river environments, we have attempted to generalize the ways in which the traits of engineer plant species constrain physical ecosystem engineering outcomes along three main vegetation development pathways. Our extended conceptual model of island development identifies three interacting aspects of the river system that may constrain the functioning and relative importance of those three pathways: flow disturbance energy, windows of opportunity and local growing conditions. We hope that this conceptualization of how multiple tree species might function in different but complementary ways to drive island development will be helpful in the context of other temperate river environments dominated by the same or other riparian tree species. In addition, the conceptual model provides a clear framework that could be explored in detail using numerical models (e.g., Bertoldi et al., 2014; Caponi & Siviglia, 2018).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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