DRIVERS OF RIPARIAN TREE INVASION ON A DESERT STREAM

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ABSTRACT

Understanding mechanisms of exotic species' invasions is essential to managing riparian landscapes throughout the world. In the southwestern USA, the two most dominant invaders of riparian habitats are the exotic tree species tamarisk (*Tamarix ramosissima*, *Tamarix chinensis*, and their hybrids) and Russian olive (*Elaeagnus angustifolia*). These plants were introduced around 1900, and their success may be facilitated by river regulation, river channel changes, and precipitation patterns. We hypothesized that riparian invasion in Canyon de Chelly, Arizona, was initiated by a change point event such as plantings, dam construction, or channel incision and that establishment near a change point was tied to flood events. We aged tamarisk, Russian olive, and native cottonwood trees from study sites in Canyon de Chelly and used tree ring analysis to determine the year of establishment and the elevation of the germination point relative to the channel. We used Bayesian Poisson regression and information theoretics to identify change points and precipitation variables driving annual tree establishment. We found that most tamarisk and Russian olive trees established in the late 1980s, and most cottonwoods established in 1930-1950 and 1980-2000. Regression models indicated that change points occurred in 1983 for Russian olive and 1988 for tamarisk, and precipitation was important for establishment. Although plantings and river regulation probably played a role in tree invasion, our results suggest that these species required precipitation and stream channel change for widespread establishment in Canyon de Chelly. The factors driving riparian invasions may not be those often associated with degraded rivers, such as altered hydrographs and land management changes, thus requiring analyses of the full range of ecological and physical processes. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS: Russian olive; tamarisk; floodplains; exotic plant species; invasive species; Bayesian change point model

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INTRODUCTION

The ecological, economic, and social impacts of exotic, invasive plants on native ecosystems such as rivers and riparian areas have stimulated broad concern among researchers, land managers, and the general public (Stohlgren *et al.*, 1998; Zavaleta, 2000; Richardson *et al.*, 2007). Exotic invasive plants often exclude native plants and alter physical and ecological processes (Simberloff, 2005). Riparian areas are of particular concern because they support critical biodiversity of both plants and animals, despite covering a small percentage of the landscape (Knopf *et al.*, 1988; Sabo *et al.*, 2005). Riparian areas have also been invaded by exotic species to a greater extent than other habitats worldwide (Stohlgren *et al.*, 1998; Hood and Naiman, 2000).

In the southwestern USA, the dominant riparian plant invaders are the woody species tamarisk (*Tamarix ramosissima* Ledebour, *Tamarix chinensis* Loureiro, and their hybrids) and Russian olive (*Elaeagnus angustifolia* L.) (Friedman *et al.*, 2005a). Historically, southwestern floodplains were populated by stands of native cottonwood (*Populus* spp.) and willows (*Salix* spp.) or had relatively low plant cover compared with modern floodplains (Webb and Leake, 2006). The ability of tamarisk and Russian olive to invade the southwestern USA may be explained by differences in life history strategies between these exotic species and native ones (Di Tomaso, 1998; Reynolds and Cooper, 2010). Seeds of cottonwood and willow disperse aerially in late spring and early summer, are viable for 4 to 6 weeks to coincide with spring peak river discharge, and germinate on moist substrate (Cooper *et al.*, 2003; Rood *et al.*, 2003). In contrast, tamarisk and Russian olive seeds have longer periods of seed dispersal and viability than cottonwood and willow (Cooper *et al.*, 1999; Katz and Shafroth, 2003). Mature tamarisk and Russian olive plants can tolerate long periods without available ground water, whereas native cottonwood and willow cannot (Brotherson and Winkel, 1986; Katz and Shafroth, 2003). The formation of interspecific hybrids of *Tamarix* spp. may also have facilitated its spread in North America (Friedman *et al.*, 2008; Gaskin *et al.*, 2011).

Beginning in the late 1800s, government agencies and private landowners planted tamarisk and Russian olive for shelter belts and stream bank erosion control in the central USA (Di Tomaso, 1998; Katz and Shafroth, 2003). The US Department of Agriculture planted tamarisk in Arizona,

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New Mexico, and Nevada by 1910 (Carleton, 1914), and Russian olive was introduced in western states by 1909 (Christensen, 1963). In 1934, the US Soil Conservation Service implemented a program to control stream erosion in the Colorado River basin by planting tamarisk and Russian olive throughout the Navajo Indian Reservation (SCS, 1934). Similar to riparian erosion control projects in other regions of the world that have introduced exotic plants (Henderson, 1991; Holland-Clift *et al.*, 2011), plantings in the southwestern US have been widely reported to be the seed sources and catalysts of the tamarisk and Russian olive invasion in the western USA (Robinson, 1965; Katz and Shafroth, 2003).

In addition to plantings, humans have dramatically altered the flow regime of rivers throughout the southwestern USA with dams and flow diversion structures (Graf, 1999; Carlisle *et al.*, 2011). Southwestern rivers were historically influenced by snowmelt and rain-driven floods that reworked river beds, keeping them relatively free of vegetation (Webb and Leake, 2006). River regulation has altered natural hydrologic processes, reducing snowmelt-driven flood peaks that occur during the period of native plant seed dispersal (Stromberg, 2001). Dams are reported to favour exotic plant establishment because tamarisk and Russian olive can more easily exploit altered flow regimes than native cottonwoods and willows (Stromberg *et al.*, 2007; Merritt and Poff, 2010).

Annual precipitation is highly variable in the southwestern USA and directly influences river flood events and baseflows (Hereford and Webb, 1992; Woodhouse *et al.*, 2006). Winter snow melt and high spring stream flows create habitat for both native and exotic plants (Cooper *et al.*, 2003). Late summer rain-driven floods can allow exotic plant establishment, whereas cottonwood and willow have no viable seeds at that time. Precipitation amount and timing, in addition to plantings and dams, can influence the establishment and local distribution of exotic and native riparian trees on floodplains (Levine and Stromberg, 2001; Katz *et al.*, 2005; Birken and Cooper, 2006).

Floodplain dynamics and the formation of fluvial features can also influence riparian plant establishment (Friedman *et al.*, 1996). A stream that has frequent over-bank flooding and wide but shallow channels usually has wide, open floodplains with little woody vegetation (Friedman and Lee, 2002; Webb and Leake, 2006). Conversely, streams that rarely flood yet have shallow ground water often support dense stands of riparian vegetation that establishes after floods (Friedman and Lee, 2002). A stream that changes from one type to another, for example, from a wide, braided channel to a narrow, incised channel, may incur dramatic changes in its riparian vegetation (Johnson, 2002). Furthermore, rivers that narrow and incise can allow riparian vegetation to establish during the narrowing process (Merritt and Cooper, 2000; Webb and Leake, 2006).

Changes in flood and sediment regimes, river regulation, land use, and climate have affected patterns of riparian vegetation establishment in many areas (Friedman *et al.*, 1998; Johnson, 2002; Webb and Leake, 2006; Merritt and Poff, 2010). In Canyon de Chelly National Monument, Arizona (Canyon de Chelly) tamarisk and Russian olive plantings, dam construction, climate variation, and channel changes have all occurred in recent history. Historic photos by Ansel Adams and others showed that a broad, sandy, and unvegetated channel occurred in the early to middle 1900s, where valley bottoms are now dominated by dense stands of tamarisk and Russian olive interspersed with stands of native cottonwood (Figure 1; Cadol *et al.*, 2011). However, it is unknown which processes or events changed the landscape character and triggered tamarisk and Russian olive invasion as well as native cottonwood establishment.

The goal of our study was to analyse the role of plantings, dams, precipitation, and channel change in facilitating plant establishment and landscape change in Canyon de Chelly. We hypothesized that if invasion was initiated by a discrete change point event such as plantings, dam construction, or channel incision, the majority of plants would have
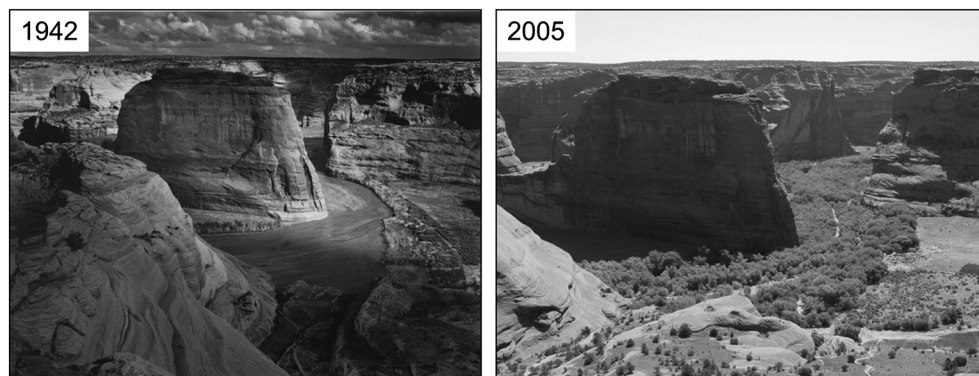

Figure 1. Chinle wash at White House Ruins overlook facing northeast, Canyon de Chelly National Monument, Arizona. Left photo is 'Canyon de Chelly, 1942' photographed by Ansel Adams© in 1942 and the right photo by D. Cooper in 2005

established following one of the change point events. We also hypothesized that in addition to discrete trigger events, establishment was tied to floods driven by precipitation. To test these hypotheses, we aged tamarisk, Russian olive, and cottonwood plants from Canyon de Chelly using dendrochronologic techniques to determine the years when plants were established. We evaluated the strength of evidence in these data with change point models representing our hypotheses. Change point models have been used widely as a statistical approach in many scientific fields (Rigaill *et al.*, 2012), and common applications in environmental studies include understanding population dynamics in wildlife or abrupt changes in hydrologic regimes (Fujisaki *et al.*, 2008; Thomson *et al.*, 2010; Zhao *et al.*, 2012). Here, we employ Bayesian change point models in a novel application to represent riparian tree establishment patterns across time.

METHODS

Study area

Canyon de Chelly National Monument is located in northeastern Arizona, within the Navajo Indian Reservation (Figure 2). The monument includes two main canyons, Canyon de Chelly and Canyon del Muerto, that have incised through the Defiance Plateau and drain the western side of the Chuska Mountains. The canyons join 8.5 km east of Chinle, AZ, forming Chinle Wash, a tributary of the San Juan River.

The Navajo Nation and the Bureau of Indian Affairs (US Department of the Interior) built Wheatfields Dam near the head of Canyon de Chelly, approximately 40 km upstream from the confluence of Canyon de Chelly and Canyon del Muerto, in 1963. Wheatfields is an off-channel dam with a storage capacity of $7\,030\,847\,m^3$. Wheatfields Dam captures flow from Wheatfields Creek, a major tributary to Canyon de Chelly, during October through March for diversion into Wheatfields Lake (Cadol, 2007). There are no long-term records of stage height or dam release flow from Wheatfields Dam (Navajo Nation Safety of Dams, pers. comm.).

The town of Chinle receives an annual average of 23.3 cm of precipitation, with an average of 13.4 cm falling during June through October, largely during late summer monsoon-driven precipitation events. Chinle Wash is an intermittent stream with a bimodal annual flow pattern. Discharge peaks occur because of spring mountain snowmelt runoff and monsoon rains.

The historic Chinle Wash streambed was wide, shallow, and braided with few riparian trees. Today, a single-threaded and deeply incised (1–5 m deep) channel occurs along most of its length with dense stands of tamarisk and Russian olive interspersed with stands of native cottonwood (Figure 1) (Rink, 2003; Cadol *et al.*, 2011).

Dendrochronologic analysis

We sampled tamarisk and Russian olive plants in four 4-ha study sites encompassing the width of the riparian plant
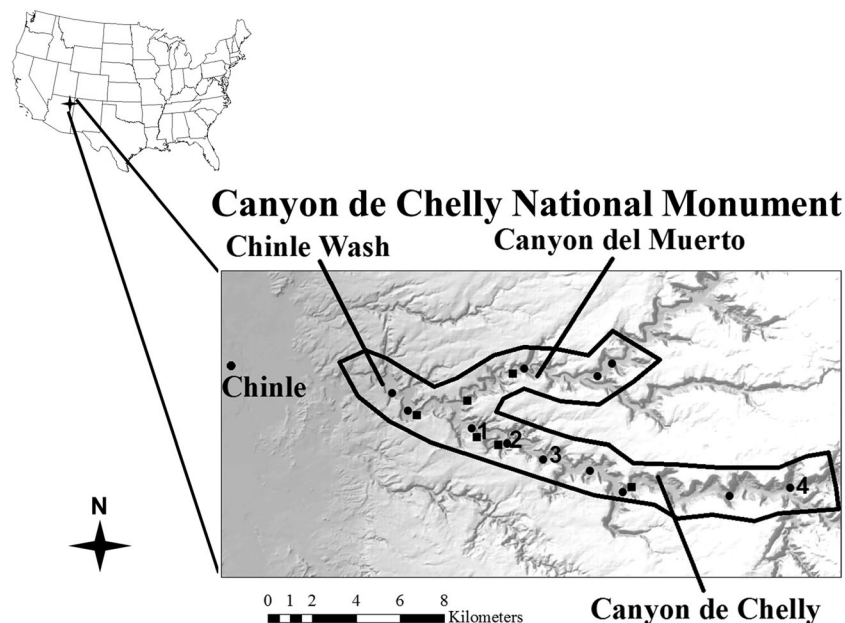

Figure 2. Map of Canyon de Chelly National Monument, Arizona, USA. The cross on the map of the USA indicates the location of Canyon de Chelly and the enlarged area. Study sites are indicated by numbers: 1—Lower White House, 2—Upper White House, 3—Sliding Rock, 4—Spider Rock. Squares indicate locations where large tamarisk and Russian olive plants were subjectively sampled, and the triangle indicates where young tamarisk and Russian olive plants were sampled. Circles indicate cottonwood tree coring sites

community adjacent to the wash in Canyon de Chelly above its confluence with Canyon del Muerto. Study sites included Lower White House, Upper White House, Sliding Rock, and Spider Rock (Figure 2). One transect was established in each study site, perpendicular to the stream channel, that included a representative sample of all tree size classes. All exotic plants within 3 m of each transect were excavated using a backhoe and/or hand shovels. The ground surface elevation at each plant was determined by topographic surveying, and the ground surface position on each plant's trunk was marked with a nail. Excavated plants were dried, cross-sectioned with a chainsaw, and sanded. The germination point was identified as the point where the pith originated. The depth below ground surface (and elevation) of the germination point was determined by analysis of the plant cross sections and topographic survey data. Plant cross sections were analysed using a precision binocular microscope to count annual growth rings. Methods for dating tamarisk and Russian olive and identifying germination points are based on Cooper *et al.* (2003), Friedman *et al.* (2005b), and Birken and Cooper (2006).

To understand the full range of timing of woody plant invasion in Canyon de Chelly, we subjectively sampled the largest tamarisk ($N = 13$) and Russian olive ($N = 5$) we could find in Canyon de Chelly, as well as young tamarisk ($N = 7$) and Russian olive ($N = 4$) and native cottonwood trees ($N = 118$) (Figure 2). Old tamarisk and Russian olive were sampled from five sites above the confluence of Canyon de Chelly and Canyon del Muerto: two sites in Canyon del Muerto, and three sites in Canyon de Chelly. Young tamarisk and Russian olive trees were sampled from a non-incised reach of Chinle Wash, 1 km below the confluence of Canyon de Chelly and Canyon del Muerto.

Cottonwood trees were sampled in 12 large stands that appeared to have multiple size classes (<10, 10–30, 30–75, and >75 cm dbh). We sampled three sites in Canyon del Muerto, six in Canyon de Chelly, and two in Chinle Wash. Five trees in each size class were sampled at each site, using an increment borer to extract cores as close to the ground surface as possible. Cottonwood tree cores were mounted, dried, and sanded, and growth rings were counted as described above. All cottonwood ring counts represent minimum ages as they were most likely from a stem section above the germination point (Scott *et al.*, 1997). Subjectively chosen samples of tamarisk, Russian olive, and cottonwood were not used in our statistical analyses.

Climate data analysis

Snowmelt-driven or precipitation-driven floods typically trigger riparian tree establishment. Therefore, river discharge records can provide critical information on possible establishment years (Scott *et al.*, 1997; Birken and Cooper, 2006).

A US Geological Survey stream gauge was operated at the mouth of Canyon de Chelly from November 1999 to July 2006; no longer-term records of river discharge exist for Chinle Wash. The Chinle, Arizona, weather station was operated by the National Climate Data Center from 1936 to present, and we obtained daily precipitation data from the Western Regional Climate Center (http://www.wrcc.dri.edu/). For all discharge and precipitation data, we summed the daily totals to calculate cumulative water year (October through September) precipitation and discharge. We used linear regression models to analyse the pairwise relationships for water year between Chinle precipitation and stream discharge for years that they share (2000–2006, $n = 7$). There was a strong positive relationship between water year precipitation and discharge ($R^2 = 0.82$). Therefore, we used the Chinle precipitation record as a proxy for stream flow in Chinle Wash, because of its longer period of record.

Statistical modelling

To test the effect of cumulative water year precipitation on plant establishment and the potential presence of a critical change point for each species, we developed a candidate set of Bayesian regression models. Each model estimated the relationship between plant establishment and precipitation in the water year of establishment (WY_0), precipitation in the following water year (WY_{+1}), and a theoretical change point where the mechanisms driving plant establishment change abruptly. We also included a scaling 'age' variable to account for the fact that we would expect more young trees than old trees because of background mortality rates and self-thinning: age $= 1, \ldots, N_{years}$. We assumed a Poisson error structure because our data were counts including zeros (Crawley, 2007).

There are three ways that regressions based on data from multiple sites can be conducted (Gelman and Hill, 2009). The first is to treat sites as distinct, building a model for each site. This approach is undesirable because it assumes that each site is somehow unique, thereby hindering generalization. The second approach is to treat regression slopes or intercepts (or both) as random variables (a.k.a. random effects; Gelman and Hill, 2009) drawn from an overall distribution of sites. This is the most desirable approach but requires multiple sites. Four sites is the minimum for this approach (Gelman and Hill, 2009), and preliminary analyses indicated problems with convergence of hyperparameters when we attempted to use this approach. The third approach, which we used, is to conduct the analysis at the individual plant level, pooling across sites ($N = 58$ Russian olives and 72 tamarisk). We justify this approach because it allowed convergence and generalization. Future work would benefit from sampling designs with >4 sites, allowing a random effects analysis.

We developed two null models: (1) a Poisson regression with only an intercept and no predictor variables or change point and (2) a Poisson regression with precipitation and age variables but without a change point. To test the hypothesis that precipitation was important for establishment prior to a change point but not after the change point, we developed a model (3) where precipitation variables disappear after the change point but intercept and age predictor variables remain constant. Finally, we developed three additional change point regression models of increasing complexity to test the role of precipitation before and after a change point: (4) different intercepts before and after the change point but the same regressor slopes, (5) different intercepts and precipitation regressor slopes but the same 'age' slope before and after the change point, and (6) different intercepts and different regressor slopes before and after the change point (Table 1). For models 3–6, a change point year was estimated.

Models were compared using deviance information criteria (DIC) that is a generalization of Akaike Information Criteria (AIC) for Bayesian analyses (Spiegelhalter et al., 2002). Smaller values of DIC demonstrate better-fitting models. We calculated delta DIC (ΔDIC), the difference between a given model and the best (minimum DIC) model, and DIC weights (W_{DIC}) for each model (Link and Barker, 2006). W_{DIC} sum to one over a given candidate set of models and are useful for comparing the weight of evidence for one model over another, similar to AIC weights (Burnham and Anderson, 2002; Spiegelhalter et al., 2002). We calculated W_{DIC} using the following formula:

$$W_{DIC} = \frac{\left[e^{\left(-\frac{1}{2}\right)(\Delta DIC)} \right]}{\left[\sum e^{\left(-\frac{1}{2}\right)(\Delta DIC)} \right]}$$

where the numerator is calculated for the given model and the denominator is the sum over all models in the candidate set (Farnsworth et al., 2006). ΔDIC and W_{DIC} are more easily interpretable than raw DIC values.

We evaluated model fit using posterior predictive checks (Gelman et al., 2004; Gelman and Hill, 2009). Posterior predictive checks calculate a test statistic from the observed data and from simulated data from the model. We tested for lack of model fit by calculating a Bayesian P-value (P_B) from the test statistics, which is the probability that the simulated data are more extreme than the observed data. We calculated P_B for the mean (P_{B-mean}), standard deviation (P_{B-SD}), and coefficient of variation (P_{B-CV}) for the observed and simulated data. A model shows lack of fit if P_B is close to 0 or 1 (Gelman et al., 2004).

All statistical analyses were conducted in the R program version 2.12.2 (R Development Core Team, 2011). Bayesian analyses were run from R using JAGS (Plummer, 2003, 2010).

RESULTS

The majority of tamarisk and Russian olive trees in our study sites were established in the late 1980s (Figure 3). The oldest tamarisk in our study sites was established in 1974 and the oldest Russian olive in 1966. For both

Table I. Candidate models and results of Bayesian regression models relating tamarisk and Russian olive establishment in Canyon de Chelly to water year precipitation (WY) and in the year following establishment (WY$_{+1}$)

Model	DIC	ΔDIC	W_{DIC}
Russian olive			
(1) $a + $Age	131.9	44.47	0.000
(2) $a + WY + WY_{+1} + $Age	110	22.57	0.000
(3) $a + ($WY$ + WY_{+1})(1_{t<CP}, 0_{t>CP}) + $Age	100.4	12.97	0.001
(4) $(a1_{t<CP}, a2_{t>CP}) + bWY + cWY_{+1} + d$Age	**87.43**	**0**	**0.758**
(5) $(a1_{t<CP}, a2_{t>CP}) + (b1_{t<CP}, b2_{t>CP})WY + (c1_{t<CP}, c2_{t>CP})WY_{+1} + d$Age	91.02	3.59	0.126
(6) $(a1_{t<CP}, a2_{t>CP}) + (b1_{t<CP}, b2_{t>CP})WY + (c1_{t<CP}, c2_{t>CP})WY_{+1} + (d1_{t<CP}, d2_{t>CP})$Age	91.2	3.77	0.115
Tamarisk			
(1) $a + $Age	156.4	61.34	0.000
(2) $a + WY + WY_{+1} + $Age	157.5	62.44	0.000
(3) $a + ($WY$ + WY_{+1})(1_{t<CP}, 0_{t>CP}) + $Age	149.0	53.94	0.000
(4) $(a1_{t<CP}, a2_{t>CP}) + bWY + cWY_{+1} + d$Age	102.1	7.04	0.028
(5) $(a1_{t<CP}, a2_{t>CP}) + (b1_{t<CP}, b2_{t>CP})WY + (c1_{t<CP}, c2_{t>CP})WY_{+1} + d$Age	103.7	8.64	0.013
(6) $(a1_{t<CP}, a2_{t>CP}) + (b1_{t<CP}, b2_{t>CP})WY + (c1_{t<CP}, c2_{t>CP})WY_{+1} + (d1_{t<CP}, d2_{t>CP})$Age	**95.06**	**0**	**0.959**

Models included (1) an intercept and an age variable; (2) an intercept, WY, WY$_{+1}$, and age variables but no change point; (3) a change point (CP) variable that is 1 before the change point ($t <$ CP) and 0 after the change point ($t >$ CP) causing precipitation variables to disappear after the change point but intercept and age variables remain constant; (4) different intercepts before and after the change point but the same regressor slopes; (5) different intercepts and precipitation regressor slopes but the same 'age' slope before and after the change point; and (6) different intercepts and different regressor slopes before and after the change point. Models are shown with DIC, change in DIC from the best model (ΔDIC), and DIC weight (W_{DIC}).
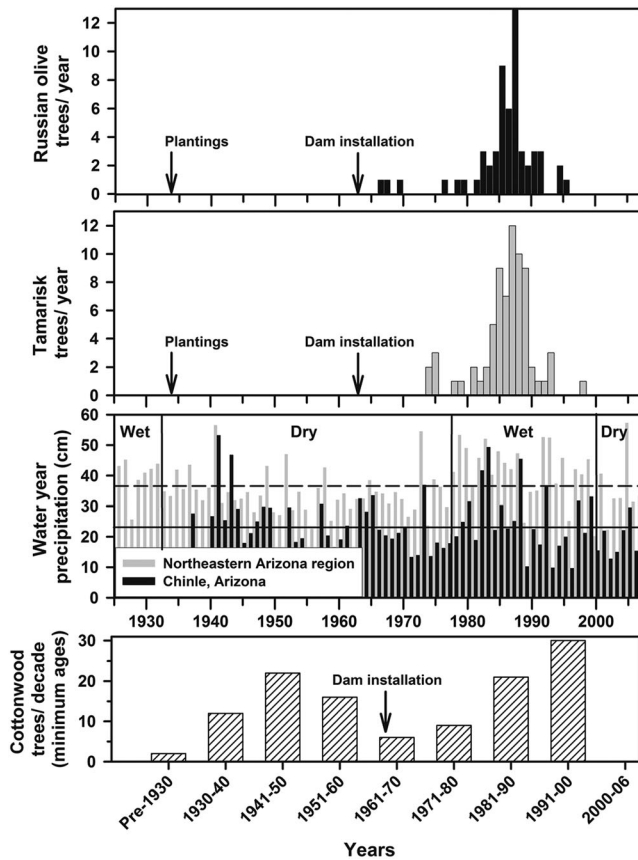
Figure 3. Top two panels: the number of Russian olive trees (black bars) and tamarisk trees (grey bars) that established each year in Canyon de Chelly. Plantings in 1934 and dam installation in 1963 are indicated with arrows. Middle bottom panel: Northeastern Arizona regional water year precipitation (cm) for years 1925–2006 (grey bars) with long-term average noted with a dashed line (36.7 cm) and total water year precipitation for Chinle for years 1936–2006 (black bars) with long-term average indicated by a solid line (23.3 cm). Wet and dry periods are noted in the middle bottom panel as consecutive years with multiple above-average or below-average precipitation. Bottom panel: the number of cottonwoods establishing in Canyon de Chelly in 10-year time periods from 1930 to 2006

tamarisk and Russian olive, models that included and estimated a change point year performed substantially better than the null models (Table 1). Posterior predictive checks for best models indicated good fit: The models simulated data that were consistent with the observations resulting in P_B values near 0.5 (Russian olive best model: $P_{\text{B-mean}} = 0.5$, $P_{\text{B-SD}} = 0.53$, and $P_{\text{B-CV}} = 0.57$; tamarisk best model: $P_{\text{B-mean}} = 0.5$, $P_{\text{B-SD}} = 0.55$, and $P_{\text{B-CV}} = 0.61$).

For Russian olive, model 4, with different intercepts before and after the change point year but the same precipitation and age regressors, emerged as the best model with a DIC weight of 0.758, indicating that 75% of the weight of evidence favoured this model (Tables 1 and 2). However, the two more complex models that also included a change

Table II. Parameter and measures of model fit (SD = Standard deviation, LCI = Lower 95% Confidence Interval, UCI = Upper 95% confidence interval) estimates for the best models (lowest DIC, Table 1) for estimating annual Russian olive and tamarisk establishment

Model	Parameter	Estimate	SD	LCI	UCI
Russian olive					
(4)	$a1$	−0.11	0.52	−1.20	0.85
	$a2$	2.67	0.88	0.92	4.37
	b	0.44	0.17	0.08	0.75
	c	0.58	0.11	0.37	0.79
	d	−0.07	0.04	−0.14	0.01
	Change point year	1983.5	0.48	1982.4	1984.7
Tamarisk					
(6)	$a1$	−1.16	0.52	−2.24	−0.19
	$a2$	7.23	2.84	1.58	12.75
	$b1$	−0.30	0.21	−0.73	0.09
	$b2$	−0.80	0.51	−1.86	0.08
	$c1$	−0.11	0.17	−0.51	0.18
	$c2$	−0.38	0.48	−1.45	0.45
	$d1$	0.26	0.05	0.16	0.36
	$d2$	−0.40	0.15	−0.70	−0.11
	Change point year	1988.3	0.84	1986.2	1989.8

point (5 and 6 in Table 1) were within four DIC points with weights of 0.126 and 0.115, indicating that those models also performed well. For models 4, 5, and 6, the change point year was estimated to be 1983, 1983, and 1984. A change point year of 1983 was identified as the beginning of the large pulse of Russian olive establishment that started in 1983 and peaked in 1985 through 1987 (Figure 3). Nearly 50% of the sample trees were established in 1985, 1986, and 1987.

For tamarisk, model 6, with different intercepts, different precipitation and age regressors before and after the change point year, emerged as the best model with a DIC weight of 0.95, indicating that 95% of the weight of evidence favoured this model over the other candidates (Tables 1 and 2). For model 6, the change point year was estimated to be 1988 at the end of the tamarisk establishment pulse that occurred from 1984 to 1989 (Figure 3) when 63% of sample trees were established.

Average annual precipitation for Chinle during the period of record 1930 to 2006 was 23.3 cm, and average precipitation for the northeastern Arizona region was 36.7 cm (Figure 3). A linear regression model between annual water year precipitation in Chinle and northeastern Arizona indicated a positive relationship (Estimate = 0.59, $t = 6.85$, $P < 0.001$, and $R^2 = 0.40$, $F_{1,69} = 46.92$, $P < 0.001$). Long-term precipitation records for northeastern Arizona indicate periods of consecutive years of above-average (wet) and below-average (dry) precipitation that match patterns of precipitation in Chinle. A wet period occurred between 1905 and 1931, a dry period occurred from 1932

to 1978, and another wet period occurred from 1978 to 2000 (Figure 3).

Within-site alluvial sediment thickness above the root crown averaged 7.7 ± 0.8 cm (mean $\pm$ SE) at Lower White House, 7.7 ± 0.6 cm at Upper White House, 6.4 ± 1.3 cm at Sliding Rock, and 30.6 ± 3.7 cm at Spider Rock. Thus, little sediment accumulated on the Lower and Upper White House and Sliding Rock floodplains after the majority of plants were established. The cross-sectional area of study transects was similar between sites, with the oldest plants established along the abandoned flood plain margins and younger plants established closer to the current incised channel (Figure 4). No tamarisk or Russian olive was established on the floodplain in our sites after 1998.

Most of the large plants sampled outside of our intensive study sites in Canyon de Chelly had rotten centres, and it was only possible to establish minimum ages. The oldest tamarisk was established at the latest in 1949, although it is likely much older, and Russian olive was established at the latest in 1964 (minimum ages). The youngest plants outside of our intensive study sites were established adjacent to the stream channel in 1999 through 2002.

The majority of cottonwoods from Canyon de Chelly had establishment years (minimum ages) dating to the 1940s and the 1980–1990s (Figure 3). Tree age at ground surface and true age at the root crown varied by a mean of 7 years on the Missouri River, Montana (Scott *et al.*, 1997). Because our tree cores were collected near the ground surface, our age estimates for trees greater than 20 years old are likely underestimates. Trees with ring counts indicating establishment in the 1930s or 1940s were likely established between 1920 and 1930.

DISCUSSION

The majority of tamarisk and Russian olive in our study sites did not establish from purposely-planted individuals.
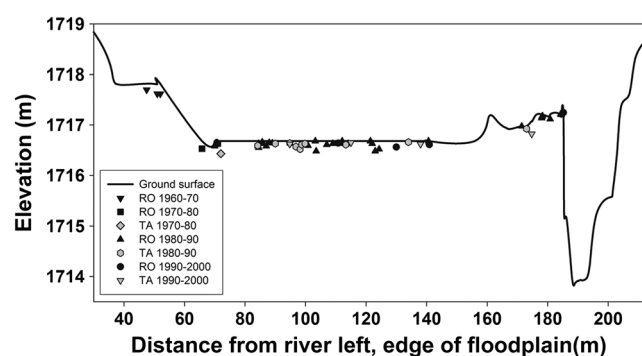

Figure 4. Cross-sectional elevation of the main wash at Lower White House Site facing downstream. The solid line indicates ground surface, and symbols indicate plant species, ages, and locations: grey shapes indicate tamarisk (TA) and black shapes indicate Russian olive (RO)

Instead, they were established from dispersing seeds between the years 1985 and 1989. This invasion is recent compared with other regions of the southwestern USA where tamarisk invasion occurred from the 1920s through the 1950s (Robinson, 1965; Graf, 1978; Birken and Cooper, 2006). Because most plant establishment occurred long after the purposeful plantings in the 1930s and dam construction in the 1960s, it indicates that although these events may have facilitated some plant establishment, they were not the primary triggers of the massive exotic plant invasion of the 1980s. Our analysis suggests that change points occurred at the beginning, for Russian olive, and at the end, for tamarisk, of the major establishment period for these species and was driven by a period of high precipitation.

Cottonwood establishment in Canyon de Chelly appears to be related to past wet and dry periods in northeastern Arizona (Figure 4). Climate reconstructions based on dendrochonological analyses of non-riparian trees in the upper Colorado River basin have shown that the end of the 19th century was characterized by drought, with an abrupt transition to an extreme wet period between 1905 and the 1920s (McAuliffe *et al.*, 2006; Woodhouse *et al.*, 2006). Precipitation records for northeastern Arizona and flow reconstruction for the Escalante River in southeastern Utah corroborate this pattern of consecutive years of above-average precipitation between 1905 and 1933 (Figure 4; Webb *et al.*, 1988). In northeastern Arizona, the period between 1932 and 1978 included consecutive decades of below-average precipitation, and the period between 1978 and 2000 had consecutive decades of above-average precipitation (Figure 4). We expected more young than old cottonwood trees because of natural mortality (self-thinning). However, most cottonwoods in our sample population had approximate establishment years from 1930 to 1950 and 1980 to 2000 (Figure 3). The early pulse of cottonwood establishment appears to correspond with the regional wet period between 1905 and 1930. The later pulse corresponds with the wet period in the 1980s that also triggered widespread Russian olive and tamarisk establishment.

The oldest tamarisk and Russian olive found in our study sites were established from dispersing seeds in 1966, and the oldest in Canyon de Chelly were established by at least 1949. These dates are surprisingly recent considering that thousands of tamarisk and Russian olive were planted in Canyon de Chelly during the 1930s (SCS, 1934). Tamarisk are known to flower and produce seeds when as young as 2 years old, and tamarisk populations established and expanded rapidly along other rivers in the region in the 1930s (Graf, 1978; Di Tomaso, 1998). An aerial photograph analysis of riparian vegetation cover change in Canyon de Chelly from 1935 to 2004 indicated that riparian tree cover increased slowly between 1935 and 1981 but increased dramatically after 1981 (Cadol *et al.*, 2011). Therefore, the

1930s plantings likely failed to establish and persist as few if any individuals from these cohorts survive today, and vegetation cover did not greatly increase in response to or immediately following the plantings. The few individuals from the old plantings that did survive likely served as a seed source for the later invasion.

There is no evidence that tamarisk and Russian olive occurred in Canyon de Chelly prior to the 1934 plantings. However, it is possible that tamarisk arrived via aerially dispersed seed from populations elsewhere in the region during or prior to the 1930s and could have already been present when the plantings occurred (Carleton, 1914; Graf, 1978). In contrast, Russian olive was not widespread in the region in 1930. It was introduced later than tamarisk, and compared with tamarisk's tiny wind-borne propogules, the large, heavy seeds from Russian olive trees are thought to spread more slowly across the landscape (Friedman *et al*., 2005a). Therefore, the 1930s plantings in Canyon de Chelly could have been the first introduction of Russian olive in the area.

If tamarisk and Russian olive invasion had been triggered by reduced peak stream flow caused by the installation of Wheatfields Dam near the top of Canyon de Chelly, we expected to find significant establishment during the 1960s and 1970s, relatively soon after dam construction, and decreases in cottonwood establishment following the 1960s (Stromberg *et al*., 2007; Merritt and Poff, 2010). Because Wheatfields Dam is off-channel and it captures water draining less than half of the Canyon de Chelly watershed, and only during winter months, it likely has little impact on sediment yield, spring runoff, or monsoon-driven flows in Canyon de Chelly. There was no direct link between dam installation and tamarisk, Russian olive, and cottonwood establishment patterns.

Saline soils may favour the more salt-tolerant tamarisk and Russian olive over native cottonwood establishment (Di Tomaso, 1998; Glenn *et al*., 1998). However, we did not test soil salinity because salt concentrations on the active floodplain prior to incision were likely low because of frequent flooding of the sandy soils (Jolly *et al*., 1993) and as indicated by the ability of cottonwoods to establish in sites throughout the canyons. It is likely that more salts have accumulated in the abandoned floodplain areas with tamarisk and Russian olive than in areas with cottonwood; however, we did not observe notable salt accumulation in these stands. If increases in soil salinity occurred, it happened gradually after tree establishment and likely was not a factor influencing establishment patterns (Lesica and DeLuca, 2004; Merritt and Shafroth, in press).

During the 1970s, all but three years had below-average annual precipitation. However, 1982 and 1983 were exceptionally wet years in the region, with above-average snow pack that likely produced large spring floods in Canyon de Chelly, as they did in the nearby Grand Canyon, Arizona (Mortenson *et al*., 2011). The years from 1984 to 1988 all had average or above-average annual precipitation that also likely led to widespread flooding that triggered riparian tree establishment in Canyon de Chelly (Figure 3).

Riparian tree establishment from dispersing seeds during the mid-to-late 1980s coincides with the period when Chinle Wash narrowed and incised (Cadol *et al*., 2011). It is our hypothesis that channel incision in the late 1980s facilitated the survival of the mid-to-late 1980s cohort of riparian tree seedlings. Prior to channel incision, annual flooding and braided channel dynamics in Chinle Wash would have scoured most seedlings from the streambed and limited survival, including plantings, and maintained the broad, barren sandy channel as shown in photographs from the early 1900s (Figure 1; Cadol *et al*., 2011).

Although the exact timing and rate of channel incision is unknown, it is clear that channel narrowing occurred between aerial photographs taken in 1981, 1989, and 2004 (Figures 3 and 4 in Cadol *et al*., 2011). By 2004, channel narrowing had ceased in our study reaches, but channel incision continued to occur. Valley cross-sectional data indicate that tamarisk and Russian olive were established on an active flood plain that was subsequently abandoned because of stream incision (Figure 4) (Jaeger and Wohl, 2011). Because both tamarisk and Russian olive seeds germinate on or very close to the soil surface, the thin sediment layers deposited over their germination points indicate that little flooding occurred after seedling establishment. This was most likely caused by channel incision around the time of seedling establishment. By 2005, the stream channel was at least 2 m below the germination point of most analysed plants, suggesting that incision occurred after plant establishment because flood waters were no longer reaching the floodplain surface.

High precipitation during 1982 through 1988 (Figure 3) created large spring and summer flood events that provided suitable substrate for riparian plant germination. These conditions occurred throughout the region in the 1980s and provided excellent conditions for tamarisk establishment on other regional rivers (Mortenson *et al*., 2011). These precipitation patterns appear to have occurred coincidentally with the timing of stream incision, allowing newly established plants to be safe from flood erosion as streams in Canyon de Chelly cut 2–3 m deep into their floodplains and the channel changed from a braided to meandering type. Riparian plants provided bank stability that could have exacerbated stream bed narrowing and incision (Jaeger, 2009; Pollen-Bankhead *et al*., 2009). However, the direction of causality remains unclear: did incision facilitate plant survival or did dense riparian vegetation cause channelization of flow and trigger incision?

Plantings and river regulation by the dam may have played a role in tamarisk and Russian olive invasion by providing a local seed source and a slightly altered hydrograph. However, our results suggest that the large scale invasion event was triggered by a combination of natural precipitation drivers and stream bed adjustments rather than the effects of plantings or river regulation alone. Plant invasion depended upon a sequence of years with above-average precipitation in combination with stream incision that allowed seedlings to be safe from erosion by subsequent flood events. As we found in Canyon de Chelly, the factors driving invasions may not be those often associated with degraded rivers such as altered hydrographs and sediment budgets. Both exotic species and native cottonwood were able to take advantage of suitable hydrologic and geomorphic conditions to establish from dispersing seeds. Rivers across the southwestern USA often support riparian vegetation that establishes in pulse events when floodplain and streamflow conditions are ideal (Friedman and Lee, 2002; Mortenson *et al.*, 2011). Exotic tree invasions worldwide, and especially along rivers, depend on multiple physical and biological factors to facilitate establishment and spread (Friedman and Lee, 2002; Cooper *et al.*, 2003; Lamarque *et al.*, 2011). Therefore, analysis of a wide range of ecological and physical processes is required to understand broad-scale riparian tree establishment patterns.

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