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Threshold dynamics in plant succession after tree planting in agricultural riparian zones

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Threshold dynamics in reforested riparian zones

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Summary

1. Trajectories of plant communities can be described by different models of plant succession. While a clementsian (gradual continuum model) or gleasonian approach (relay floristics model) have traditionally been used to inform restoration outcomes, alternative succession models developed recently may better represent restoration trajectories. The threshold dynamics succession model, which predicts an abrupt species turnover after an environmental threshold is crossed, has never been used in a restoration context. This model might, however, better describe shifts in plant competitive ranking and facilitation interactions during species turnover.

2. Fifty-three riparian zones, planted with trees 3 to 17 years prior to sampling, and 14 natural riparian forests were studied in two agricultural watersheds of south-eastern Québec (Canada). The cover of vegetation strata was assessed at the site-scale, and the cover of plant species was estimated in a total of 784 1-m² plots. Canopy cover was measured stereoscopically for each plot.

3. As revealed by Principal Response Curves (PRC) and broken stick models, herbaceous species composition was stable during the first 12–13 years after tree planting, but then abruptly shifted. This two-step pattern in species turnover followed the increase of canopy cover after tree planting. Once canopy cover passed a threshold of ca 40%, plant succession started and led to the re-establishment of forest communities 17 years after planting.

4. Following herbaceous species turnover, the cover of ecological groups changed significantly toward covers of natural riparian forests: shade-tolerant species generally increased while light-demanding and non-native species decreased. Vegetation
structure was also significantly affected by tree planting: tree and shrub cover increased while monocot cover decreased.

5. Synthesis and applications. Tree planting efficiently restored herbaceous forest communities in riparian zones by inducing a species turnover mediated by light availability corresponding to threshold dynamics model in plant succession. Fostering and monitoring canopy closure in tree-planted riparian zones should improve restoration success and the design of alternative strategies. The innovative statistical approach of this study aiming to identify succession patterns and their associated theoretical models can guide restoration in any type of ecosystem around the world to bridge the gap between science and management.

Key-words
Agricultural landscapes, canopy cover, herbaceous communities, light availability, resilience, restoration ecology, riparian zones, succession models, vegetation recovery

1. Introduction
Succession models inform our understanding of ecosystem dynamics by predicting the resilience of ecosystems, their response to disturbances and the underlying assembly rules of plant communities (Young, Petersen & Clary 2005; Hobbs & Suding 2009; Alday & Marrs 2014). For degraded plant communities, succession models are helpful tools to first assess restoration trajectories, and then define achievable restoration goals or design adaptive restoration practices (Hobbs & Suding 2009). Traditionally, two succession models have been used to interpret restoration outcomes: (i) gradual continuum models based on a clementsian view of plant communities predicting a deterministic linear species turnover proportional to
environmental changes (Clements 1916), and (ii) relay floristic models based on a
gleasonian approach predicting a sequential replacement of species through autogenic
facilitation and inhibition interactions (Gleason 1926; Connell & Slatyer 1977).
More recently, emerging theoretical frameworks have however conceptualized
alternative succession models (Hobbs & Suding 2009). In particular, threshold
dynamics models which predict an abrupt shift of species composition when an
environmental threshold is crossed might be particularly relevant to evaluate
restoration trajectories and improve or redesign restoration strategies (Bestelmeyer
2006; Groffman et al. 2006; Suding & Hobbs 2009). In this context, time-series
analyses are powerful tools that can reveal temporal patterns of species dynamics. By
targeting relative species turnover against a reference system, Principal Response
Curves (PRC; Van den Brink & Ter Braak 1999) are a particularly relevant approach
to compare restoration strategies (Vandvik et al. 2005), identify the species driving
community dynamics (Poulin, Andersen & Rochefort 2013) and detect alternative
states (Alday & Marrs 2014). Furthermore, PRC might also have the potential to
reveal the succession model involved in species turnover after restoration, but have
never been used with such objective.
In forest restoration, the introduction of nurse species is a widely used passive
strategy based on a gleasonian approach (Byers et al. 2006; Padilla & Pugnaire 2006;
Gómez-Aparicio 2009). Nurse species are indeed assumed to modify abiotic
conditions (e.g. light availability, nutrient content, etc.) and create new ecological
niches suitable for the gradual spontaneous recolonization of desired species (Hobbs
& Suding 2009; Paquette & Messier 2010; McClain, Holl & Wood 2011). Yet
introducing a nurse species is not a guarantee that passive recolonization will occur.
While planting trees in riparian forests can induce a shift in herbaceous species
composition after 10 to 15 years (e.g. McClain, Holl & Wood 2011; Harris et al. 2012), the entire community usually fails to re-establish. As a result, desired recalcitrant species must be actively introduced once the canopy has developed closure (Brudvig, Mabry & Mottl 2011; McClain, Holl & Wood 2011). Given that herbaceous vegetation is a critical component of ecosystem functions and dynamics (Nilsson & Wardle 2005; Gilliam 2007), these partial restoration successes call for more research on herbaceous dynamics after tree planting. The decrease of light availability after tree planting which is a major driver for the recolonization of herbaceous species (Barbier, Gosselin & Balandier 2008; Harris et al. 2012), may act as a key environmental threshold for species turnover. Despite being previously described in rangelands (Friedel 1991), threshold dynamics models have never been investigated as potential models to inform succession of herbaceous species in tree-planted agricultural riparian zones, and design restoration strategies accordingly.

In agricultural landscapes, multiple large-scale environmental factors related to intensive land use such as habitat fragmentation and intensive use of fertilizers and pesticides can impact restoration trajectories and outcomes (Allan 2004; Tscharntke et al. 2005). Such land-use intensification could cause the low recolonization of herbaceous species and the establishment of alternative stable states through a number of processes including the impoverishment of the regional species pool (Brudvig 2011), the homogenization of local abiotic conditions (Vellend et al. 2007), the decrease of landscape connectivity (Tscharntke et al. 2005) and the limitation of plant dispersal (Hermy & Verheyen 2007). In riparian systems, however, the spatial connectivity provided by water flows generally overcomes dispersal limitation, at least for hydrochorous species (Tabacchi et al. 1998; Nilsson et al. 2010). Riparian plant species can be expected to passively recolonize ecosystems through water...
dispersal once their ecological niches have been restored (Field of Dreams Hypothesis, “if you build it, they will come”; Palmer, Ambrose & Poff 1997). However, in degraded riparian zones, hydrological connectivity also contributes to the high prevalence of biological invasions (Richardson et al. 2007) which are among the primary drivers of the establishment of non-desired alternative stable states (Suding, Gross & Houseman 2004; Didham et al. 2005). Identifying potential ecological thresholds driving species turnover and possibly leading to alternative states can not only inform theories of plant succession, but also the restoration of forested riparian zones in intensively managed agricultural landscapes.

Therefore, the goal of this study was to assess the successional trajectory followed by herbaceous communities after tree planting in riparian zones of agricultural landscapes. We propose to use for the first time a combination of statistical approaches including PRC to provide a mechanistic interpretation of riparian community assemblages over time. We predicted that tree planting would initiate a plant succession leading to the re-establishment of forest herbs after the crossing of an ecological threshold in canopy cover. Besides species composition, we evaluated whether tree planting re-established an herbaceous vegetation characteristic of natural riparian forests in terms of vegetation structure and herbaceous ecological groups.

2. Materials and methods

2.1. Study area

This study was conducted in two agricultural watersheds of south-eastern Québec (Canada; Appendix S1 in Supporting Information). The Boyer watershed (46°41' N 70°55' W) is a 216-km² area mainly devoted to agriculture (66% of land use), with scattered forest fragments (24% of land use). Between 1948 and 1992, some 73% of
the 251 km of rivers flowing through the area were channelized to increase soil

drainage and improve cultivation of annual crops (e.g. wheat, corn and soybean). On

this watershed, annual crops represent 26% of agricultural land use (OBV Côte-du-
Sud/GIRB 2011). The Bélair watershed (46°26' N 70°56' W) is a 43-km² area with a

high cover of forests (66% of land use). Agricultural production covers 14 km² (or

33%) of this watershed, of which 18% is devoted to annual crops (MAPAQ

unpublished data). Besides channelization, signs of riverbank erosion were also

identified during field work along the studied river reaches. To mitigate

environmental degradations caused by agricultural intensification and improve the

provision of ecosystem services, agricultural practices were banned on a buffer of at

least 3-m wide along streams (Gouvernement du Québec 1987). From 1995 to 2009,

extensive tree planting projects in riparian zones were conducted by local

stakeholders of the two studied watersheds. The primary objective of tree planting

was to increase water filtration and reduce soil erosion rather than to recover riparian

trees such as natives Salix or Populus spp. Consequently, the most frequently planted

tree species corresponded to Fraxinus pennsylvanica Marsh., Acer saccharum Marsh.,

Picea glauca (Moench) Voss, Larix laricina (Du Roi) K. Koch, Quercus rubra L. and

Quercus macrocarpa Michx., all natives in the study area. Planting techniques were

generally uniform over time and consisted in the planting of 30-cm tall trees in bare

soil every 3–5 m along a single row on the flat edges of agricultural fields (i.e. on

average 5m away from the field margins) without replacement of dead trees in the

successive years.

2.2. Sampling design
During the summer of 2012, 53 riparian zones representing a chronosequence of 3 to 17 years after tree planting were sampled along relatively uniform rivers (in terms of width and flow) within the two watersheds studied (Appendix S1). To ensure site representativeness and uniformity in local environmental and agricultural conditions, four conditions had to be met by a tree-planted riparian zone in order to be sampled, i.e. (i) measure at least 40 m long, (ii) have been planted with trees within a single year, (iii) be adjacent to an agricultural field with uniform crops, (iv) have a uniform vegetation structure. As a space-for-time substitution was used to assess the temporal dynamics of riparian plant communities after tree planting, sites were also selected to obtain a complete sampling of the 3–17 year chronosequence uniformly distributed over the study area. In addition to these 53 tree-planted riparian zones, 14 mature natural riparian forests were also sampled as reference ecosystems. These natural forests corresponded to the last remnants of natural riparian habitats occurring throughout the study area and were generally dominated by *Fraxinus pennsylvanica*, *Acer saccharum* and *Quercus* spp., which were also among the most frequently planted tree species.

2.3. Botanical surveys

Vegetation structure was assessed at each site by recording the cover of tree (> 5 m high), shrub (1–5 m), dicot herbs, monocot herbs (hereafter Dicots and Monocots) and pteridophyte strata using the Braun-Blanquet index (0.5: < 1% cover; 1: 1–5% cover; 2: 5–25% cover; 3: 25–50% cover; 4: 50–75%; 5: > 75% cover). Two surveys of vegetation structure were conducted along the entire length of each sampling site, the first along the flat edge of the agricultural field where trees were planted, the second along the spontaneous (unplanted) plant communities of the sloped riverbanks.
Herbaceous composition was sampled by visual estimation of species cover (%) in 1-20 m² plots along equidistant transects perpendicular to the river from the field edge to the riverbank. Canopy cover (%) over plots was estimated based on stereoscopic measurements taken at a height of 1-m height above ground level (24 MP DSLR System and WinSCANOPY software, Regent Instruments Inc., Québec, Canada). To obtain an accurate botanical survey accounting for the intra-site variability of plant communities, the number of transects at each site was proportional to the site length and the number of plots along each transect proportional to the transect length. More precisely, plant communities were sampled along two (sites shorter than 100 m) to five transects (sites longer than 200 m; max length: 1150 m) per site, into two 1-m² plots (transect shorter than 5 m; one plot on the field edge, one on the riverbank) to six equidistant plots (transect longer than 40 m; the number of plots on the field edge and on the riverbank depended on slope break) along each transect (Appendix S2).

Since a preliminary principal component analysis showed a different species composition for field edges and riverbank plots (Appendix S3), all subsequent analyses were conducted separately for these two communities. Consequently, a community-weighted mean of species cover from all plots was calculated separately for the field edge and the riverbank of each site. Two observations of plant species abundance were thus obtained per site.

Herbaceous plant species inventoried were then classified into six ecological groups related to their light requirements (shade-tolerant vs. light-demanding species), their origin (native vs. non-native) and their wetland status (wetland obligate vs. wetland facultative) based respectively on local floras (Marie-Victorin, Brouillet & Goulet 1995), the data base of Vascular Plants of Canada (Brouillet et al. 2010) and governmental classification (MDDEP 2012). These three types of species grouping
were selected considering their potential response to restoration, i.e. (i) canopy
closure after tree planting is likely to increase the shade levels experienced by
herbaceous species, (ii) colonization by native species is a desirable outcome of a
restoration project, and (iii) wetland obligates and facultatives are characteristic
species of riparian forests that might benefit from restoration. Among the 203
herbaceous species inventoried in the 784 1-m² plots within the 67 sampled riparian
zones, 26% were shade-tolerant and 74% light-demanding, 61% native and 39% non-
native, 23% wetland obligate and 15% wetland facultative (62% were non-wetland
species; Appendix S4). The total cover of these six groups was then calculated for the
field edge and riverbank of each site as the sum of covers of the corresponding
species.

2.4. Statistical analysis

Plant succession in herbaceous riparian communities after tree planting was evaluated
with a PRC, using natural riparian forests as a comparison benchmark. Site scores
along the PRC axis were then used in a broken stick regression against the time
elapsed since tree planting to identify threshold in species turnover (Toms &
Lesperance 2003). Compositional differences between tree-planted riparian zones and
natural riparian forests were assessed based on a linear mixed model with site scores
along the PRC axis as response variable, treatment (tree-planted riparian zones vs.
natural riparian forests) and the time the elapsed since tree planting (in years) as
explanatory variables and site as random factor; a Bonferroni correction was applied
to assess the significance of each contrast, here α = 0.0056 (see also Alday & Marrs
2014). Indicator species of natural riparian forests were also identified using IndVal
analysis (Dufrêne & Legendre 1997) to assess whether these species were positively
correlated with the PRC axis and thus re-established after tree planting. For each ecological group (shade-tolerant, light-demanding, native, non-native, wetland obligate and wetland facultative), a mean score along the PRC axis was finally calculated from the scores of its associated species, to evaluate ecological mechanisms likely to drive species turnover after tree planting. The existence of thresholds in the temporal dynamic of canopy cover with the time elapsed since tree planting was assessed using a binary segmentation which enables the detection of multiple thresholds (Killick, Fearnhead & Eckley 2012), followed by an ANOVA and Tukey post-hoc tests to evaluate the significance of the detected thresholds. A linear regression was then performed between site scores along PRC axis and canopy cover to quantify the strength of the relationship between canopy cover and species turnover, and thereby the driving role of light availability in plant succession.

The temporal evolution of cover after tree planting was assessed using a generalized linear model (GLM) followed by Tukey post-hoc tests for each of the six ecological groups (abundances expressed in %; GLM with a Gaussian distribution) and each of the five vegetation strata (abundances expressed with Braun-Blanquet indices; GLM with a Poisson distribution). We compared mean abundances for these groups between young plantations (3–12 years), old plantations (14–17 years) and natural riparian forests to verify if the threshold detected in species turnover was accompanied by changes in herbaceous ecological groups and vegetation structure.

All analyses were conducted in R version 3.1.0 (R Core Team 2014) using packages bentcableAR (Chiu et al. 2015), changepoint (Killick & Eckley 2014), indicpecies (De Caceres & Legendre 2009), and vegan (Oksanen et al. 2013).
3. Results

3.1. Dynamics of herbaceous communities

Plant succession after tree planting followed a two-step pattern in both field edge and riverbank communities where abrupt changes in species composition started 12 years ($R^2_{\text{broken stick}} = 92.97\%$) and 13 years after tree planting ($R^2_{\text{broken stick}} = 88.08\%$), respectively (Fig. 1, left). Prior to these thresholds, the composition of herbaceous riparian communities remained relatively stable and distinct from the herbaceous composition of natural riparian forests (Fig. 1, left). Once these thresholds were passed, a rapid turnover of herbaceous species occurred, leading to the re-establishment of forest plant communities at the end of the chronosequence. While noticeable species turnover began 12 to 13 years after tree planting, at least 17 years were necessary to recover herbaceous plant communities similar to those of natural riparian forests both at field edges ($t = -2.85; P = 0.0061$) and along riverbanks ($t = -2.69; P = 0.0094$; Fig. 1). Moreover, all the indicator species of natural riparian forests were characterized by high positive scores along the PRC axis (Fig. 1, middle).

The observed species turnover more precisely corresponded to the replacement of weeds, graminoids and ruderal species, like *Bromus inermis* L., *Phalaris arundinacea* L., *Equisetum arvense* L., *Artemisia vulgaris* L., and *Solidago canadensis* L. by ferns and forest herbs, such as *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *Athyrium filix-femina* (L.) Roth, *Trilium erectum* L. and *Rubus pubescens* Raf., as shown by species scores along the PRC axis (Fig. 1, middle). During this turnover, shade-tolerant species associated with natural riparian forests increased at the expense of light-demanding species, while non-native species decreased but were replaced by native species characteristic of riparian natural forests only in field edge community (Fig. 1, right). Wetland obligate and facultative species associated with natural riparian forests
contributed less to this successional pattern, with only a slight increase of obligate species in field edge communities over time.

3.2. Dynamics of canopy cover

The increase of mean canopy cover over time followed three-step dynamics structured around two thresholds both in field edges and along riverbanks ($R^2_{binary\ segmentation} = 83.68\%$ and $82.89\%$, respectively; Fig. 2). Six years after tree planting, mean canopy cover increased from 24% to 36% in field edges and from 23% to 31% along riverbanks, and then reached 59% and 64% respectively after a second more pronounced threshold after 12 years (Fig. 2). Among these two thresholds detected in mean canopy cover, only the second one corresponded to a significant increase in canopy cover measured at each site both at field edges ($F = 35.80; P < 0.0001$) and along riverbanks ($F = 44.26; P < 0.0001$; Fig. 2). Canopy cover thus followed a temporal pattern similar to that of species turnover, i.e. a fairly stable canopy cover of ca. 20–40% during the first 12 years after tree planting (with a slight decline in the first years), and then an abrupt increase to ca. 60% of canopy cover. This similar dynamic was further evidenced by a strong positive relationship between mean canopy cover and site scores along the PRC axis both at field edges ($F = 19.59; P = 0.0031; R^2 = 69.91\%$) and along riverbanks ($F = 20.83; P = 0.0026; R^2 = 71.25\%$; Fig. 3).

3.3. Dynamics of herbaceous ecological groups
The total cover of ecological groups was strongly influenced by the threshold detected in species turnover 12 to 13 years after tree planting (Table 1; Fig. 4). After this threshold, the cover of light-demanding and non-native species decreased but remained higher than in natural riparian forests both at field edges and along riverbanks, while the cover of shade-tolerant species increased to reach cover levels similar to those observed in natural riparian forests at field edges (Table 1; Fig. 4). The cover of native species peaked in old plantations of field edges while for riverbanks, it remained higher in young and old plantations than in natural riparian forests. The total cover of shade-tolerant species of around 20% along riverbanks of young plantations was mainly due to generalist species able to grow under shade, notably *Agrimonia striata* Michx, *Fragaria virginiana* Duchesne, *Onoclea sensibilis* L. and *Solidago rugosa* Mill., but not associated with natural riparian forests (Fig. 1). Wetland obligate and facultative species were sparsely affected by species turnover, except for a slight decrease of wetland obligates along riverbanks.

### 3.3. Dynamics of vegetation structure

Once the 12–13 year threshold was passed, tree and shrub cover increased, whereas monocot cover decreased both at field edges and along riverbanks (Table 2; Fig. 5). However, in old plantations, a cover typical of natural riparian forest was only reached for trees at field edges, and for shrubs and monocots along riverbanks (Fig. 5). For dicots and pteridophytes, cover remained similar over time and between tree-planted riparian zones and natural riparian forests in both field edge and riverbank communities (Fig. 5).

### 4. Discussion
Plant succession of tree-planted degraded ecosystems including riparian forests has generally been framed in relay floristics models (Hobbs & Suding 2009). These autogenic succession models postulate that sequential waves of species succeed one another in a linear fashion during plant succession owing to facilitation and inhibition interactions between species (Clements 1916; Connell & Slatyer 1977). However, the species turnover observed in this study suggests that an alternative model – threshold dynamics – better explains succession in tree-planted agricultural riparian zones. Herbaceous species turnover indeed followed a two-step pattern structured around an ecological threshold occurring 12 to 13 years after tree planting. Once past this threshold, species turnover started, and the herbaceous composition of riparian communities, previously stable, shifted abruptly to a species assemblage characteristic of natural riparian forests 17 years after plantation. In addition to inducing the recolonization of riparian forest species, tree planting led to the re-establishment of a vegetation structure and an abundance of ecological groups closer or similar to natural riparian forests after crossing the threshold observed in species turnover. This first evidence of a threshold dynamic in agricultural riparian zones after tree planting sheds new light on the resilience capacity of riparian plant communities. In this study, no alternative stable state was indeed identified in riparian plant communities after tree planting. Despite high cover of non-natives in young plantations, these species which were generally introduced during the European settlement for agricultural purposes, did not aggressively invade plant communities, nor drove plant succession to novel assemblages. Previous findings of long-term experiments have also demonstrated a similar role of natives and non-natives in plant succession (Meiners 2007) where the trajectory rather depends on the chronological order of species arrival rather than on their origin (Yurkonis, Meiners & Wachholder...
Furthermore, the ecological impacts of agricultural activities such as dispersal limitation (related to habitat fragmentation) and modified abiotic conditions (especially increased nutrient availability due to fertilization) did not push riparian communities into alternative states, as previously observed (Cramer et al. 2008).

Tree planting appears sufficient to re-establish plant communities characteristic of natural riparian forests (which fail to recover in the absence of tree planting; D’Amour et al. unpublished data). Riparian zones can thus tolerate high degradation due to agricultural activities contrary to upland forest plantations, where soil compaction and low organic matter content have often been found to be critical impediments to the recovery of herbaceous diversity (Flinn & Vellend 2005; Hermy & Verheyen 2007). This high resilience of riparian plant communities might be related to regular soil re-organization caused by hydrological disturbance (González et al. 2014) and to constant inputs of propagules from the river (Tabacchi et al. 1998; Nilsson et al. 2010) that have mitigated the environmental degradation associated with agricultural land use. However, this resilience is only expressed after a critical environmental threshold has been crossed, suggesting the idea of a nonlinearity between resilience capacity and environmental conditions.

The synchrony of canopy closure and herbaceous plant succession as well as the replacement of shade-tolerant by light-demanding species after tree planting clearly identifies light availability as the main factor limiting the recovery of plant communities in agricultural riparian zones, with an ecological threshold in canopy cover above ca 40%. Similar changes attributable to light availability have previously been observed in boreal, temperate and Mediterranean forests (Gómez-Aparicio et al. 2004; Barbier, Gosselin & Balandier 2008; Cole & Weltzin 2008; Jules, Sawyer & Jules 2008). Canopy closure also resulted in increased native species cover in
Australian riparian zones four years after tree planting (Cole & Weltzin 2008; Harris et al. 2012) and led to enrichment communities 10 years after planting in hybrid poplar plantations on abandoned fields (Boothroyd-Roberts, Gagnon & Truax 2013). Besides decreasing light availability, trees have been shown to influence herbaceous communities by modifying numerous other abiotic factors such as soil moisture, soil nutrients, microbial activities or microclimate (Barbier, Gosselin & Balandier 2008).

In the context of ecological restoration, PRC has been proven to be a powerful statistical tool to identify restoration success (Vandvik et al. 2005), alternative stable states (Alday & Marrs 2014) and species involved in plant succession (Poulin, Andersen & Rochefort 2013). Our study identified an additional advantage of PRC, for identification of the succession model that best represents species turnover after restoration. In an innovative adaptation, species scores along the PRC axis were averaged for meaningful ecological groups, to bring further mechanistic insights into successional patterns. Such an understanding can be taken a step further when environmental variables are monitored simultaneously with plant communities. By comparing the temporal dynamics of environmental variables with species turnover, it is possible to easily discriminate the primary drivers of plant succession, as shown here for light availability. Restoration researchers and practitioners are thus encouraged to collect both species and environmental data in restored and reference habitats over time, in order to perform time-series analyses.

While hydro-geomorphological manipulations aiming at re-establishing the natural flow regime are considered the most efficient restoration method for recovering the ecological integrity of riparian zones (Poff et al. 1997; Rood et al. 2005), acceptance and implementation of this approach is limited by the legacies of human modifications on rivers and by the socio-economic context, especially in agricultural
landscapes of high economic value (Hughes & Rood 2003). In such a context – tree planting – the second most frequent restoration strategy of riparian vegetation reported in peer-reviewed literature (González et al. 2015), can be efficient to achieve restoration goals that maximize certain ecosystem services. For example, tree planting has been shown to influence plant succession in other types of riparian zones such as Salicaceae-dominated forests (e.g. Lennox et al. 2011) and swamps (e.g. McLane et al. 2012).

Successional trajectories remain difficult to interpret and can be misleading if the succession model is unknown, especially when a lengthy time delay occurs between restoration and species turnover. The identification of threshold dynamics and environmental driver(s) allows defining effective restoration approaches focused on pushing a system over environmental threshold(s). In agricultural riparian zones, planting fast-growing tree species to form a dense canopy appears an efficient restoration strategy to rapidly decrease light availability and thereby accelerate the passive re-establishment of herbaceous forest communities. Furthermore, active reintroduction of desired species should only be considered if plant composition remains stable after the threshold in light availability has been crossed, as dispersal limitation may occur. Since succession models inform our understanding of species turnover and underlying environmental drivers, their identification should improve restoration approaches.

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Data accessibility

Plant community and environmental data can be found at http://dx.doi.org/10.5061/dryad.b46k4

References


Chiu, G., CSIRO, CSIT Bldg, ANU Campus, Acton, ACT 2601 and Australia (2015) bentcableAR: bent-cable regression for independent data or autoregressive time series. R package version 0.3.0.


http://www2.publicationsduquebec.gouv.qc.ca/ (consulted on 2016-03-17).


**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Location of the sampled riparian zones.

Appendix S2. Sampling design of riparian communities.

Appendix S3. Species-based PCA of riparian communities.

Appendix S4. List of the species inventoried.
Field edges

- Natural riparian forests
- Tree-planted riparian zones

PRC1 (11.28%)

Riverbanks

- Dryopteris carthusiana
- Thalictrum pubescens
- Athyrium filix-femina
- Oenothera oenobila
- Clethra virginiana
- Trillium erectum
- Impatiens capensis
- Rubus pubescens

PRC1 (11.62%)

Time elapsed since tree planting (years)

- Eutrochium maculatum
- Ageratina altissima
- Poa palustris
- Solidago canadensis
- Symphoricarpos laevigatus
- Equisetum arvense
- Festuca rubra
- Phalaris arundinacea
- Bromus inermis

Shade-tolerant

- Natives
- Wetland obligates

Light-demanding

- Exotics

Wetland facultatives
Fig. 1. Compositional dynamics of herbaceous riparian communities with the time elapsed since tree planting in comparison to natural riparian forests, obtained by Principal Response Curves (PRC: left side; only species with a score along axis 1 higher than |0.2| are represented; asterisks represent significant differences in species composition between tree-planted riparian zones and natural riparian forests), broken stick regression on site scores along the PRC axis against the time elapsed since tree planting (arrows indicate thresholds in species turnover) and scores of ecological groups along the PRC axis (i.e. mean score of species belonging to each group; right side). Indicator species of natural riparian forests are indicated in bold, i.e. *Rubus pubescens* (IndVal = 0.58; P = 0.0650), *Dryopteris carthusiana* (IndVal = 0.65; P = 0.0150), *Trilium erectum* (IndVal = 0.60; P = 0.0300) and *Athyrium filix-femina* (IndVal = 0.60; P = 0.0450).
Fig. 2. Thresholds in the temporal dynamics of canopy cover (mean ± SE) in riparian zones with the time elapsed since tree planting, obtained by binary segmentation (lines represent thresholds in mean canopy cover; letters correspond to significant between-threshold differences in canopy cover measured at each site, obtained by ANOVA and Tukey post-hoc tests). Canopy cover was calculated by stereoscopic measurements taken at a height of 1 m above each plant inventory plot.
Fig. 3. Relationship between sites scores along the Principal Response Curves (PRC) axis (see Fig. 1) and mean canopy cover, obtained by linear regression.
Fig. 4. Total cover of herbaceous ecological groups (mean ± SE) in young plantations (i.e. observations dated before threshold in species turnover; see Fig. 1), old plantations (i.e. after threshold) and natural riparian forests (letters correspond to significant differences obtained by Tukey post-hoc tests).
Fig. 5. Cover of vegetation strata (mean ± SE) in young plantations (i.e. observations dated before threshold in species turnover; see Fig. 1), old plantations (i.e. after threshold) and natural riparian forests (letters correspond to significant differences obtained by Tukey post-hoc tests) based on Braun-Blanquet indices (0.5: < 1% cover; 1: 1–5% cover; 2: 5–25% cover; 3: 25–50% cover; 4: 50–75%; 5: > 75% cover).
Table 1. Differences in the total cover of herbaceous ecological groups between young plantations (i.e. observations dated before threshold in species turnover; see Fig. 1), old plantations (i.e. after threshold) and natural riparian forests.

<table>
<thead>
<tr>
<th></th>
<th>Field edge</th>
<th></th>
<th>Riverbank</th>
<th></th>
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</thead>
<tbody>
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<td></td>
<td>$F$</td>
<td>$Pr &gt; P$</td>
<td>$F$</td>
<td>$Pr &gt; P$</td>
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<td>Light-demanding</td>
<td>31.15</td>
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<td>Non-natives</td>
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<td>Wetland facultatives</td>
<td>0.98</td>
<td>0.3822</td>
<td>7.37</td>
<td>$0.0013$</td>
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Table 2. Differences in the cover of vegetation strata between young plantations (i.e. observations dated before threshold in species turnover; see Fig. 1), old plantations (i.e. after threshold) and natural riparian forests.

<table>
<thead>
<tr>
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<th>Field edge</th>
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<tbody>
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<td>$Pr &gt; P$</td>
<td>$F$</td>
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<td>0.9015</td>
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