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Successional trends in Floristic Quality

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Summary

1. Simple, conservation-relevant, plant community measures are sought by resource managers. In this context, the use of Floristic Quality Assessment (FQA) has increased exponentially over the past 30 years. FQA measures a habitat's Floristic Quality and conservation value by summarizing the relative anthropogenic disturbance tolerances of its plant species (i.e. their Conservatism). However, despite their widespread use in research, restoration and conservation work, the behaviour of FQA values in communities during succession is not understood.

2. We analysed FQA values in 10 old fields over 50 years of unaltered succession. We determined whether Floristic Quality followed a predictable increasing successional trend, assessing four specific predictions: (i) FQA values will follow an asymptotically increasing, rather than peaked or linearly increasing trajectory; (ii) field initiation treatments (abandoned as hayfield or cropfield) will not lead to long-term differences in FQA values; (iii) trajectories will be consistent regardless of the particular species composition of fields and (iv) trajectories will be robust to common variations in FQA metric formulations (non-native species, varied spatial scale).

3. In all cases, a negative exponential rise to an asymptote best described FQA value trajectories over time. Field abandonment treatments did not affect FQA value trajectories. Furthermore, trends were consistent among fields despite differences in species composition among fields. Overall, the results suggest a predictable, deterministic path for FQA values over the early- to mid-successional timeframes studied.

4. *Synthesis and applications*. Understanding the temporal behaviour(s) of Floristic Quality is necessary for setting realistic restoration goals, evaluating habitat recovery and adapting management to achieve high conservation value natural areas. By illustrating the temporal consistency of Floristic Quality metrics during succession, this article demonstrates the robustness of FQA for such uses. The FQA value trajectory described here also establishes a background trend model for expected values in recovering habitats, which will allow for the assessment of an individual habitat's progression relative to the background trend. Such comparisons *en masse* will highlight the constraints of greatest importance to community-level Floristic Quality restoration. For example, FQA values in this study were ultimately limited by Conservative understorey plant re-establishment from adjacent old-growth forest. As this is not unlike species recovery patterns observed in other habitats, it suggests that restoration practitioners would do well to focus on Conservative species.

Key-words: anthropogenic disturbance, conservation value, deterministic vs. stochastic succession, Floristic Quality Assessment, Floristic Quality Index, invasion impacts, Mean *C*, remnant flora, restoration monitoring, successional trajectory

Introduction

Successional trends in plant communities and habitat restorations are commonly tracked, studied and compared using simple measures such as diversity, structure or biomass. However, these fail to capture the properties most immediately relevant for conservation – species identity and community composition (Filippi-Codaccioni *et al*. 2010). Thus, the means to compare plant assemblages with regard to their levels of endemism, rarity, regional uniqueness, taxonomic distinctness and specialization are needed (Izco 1998; Ricotta 2004; Devictor, Julliard & Jiguet 2008; Chapman, Underwood & Clarke 2009). However, quantifying such properties in ways that allow for

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easy comparisons among sites and over time has proven difficult.

It is in this context that the use of Floristic Quality Assessment (FQA) has increased exponentially over the past 30 years (e.g. North America; LaPaix, Freedman & Patriquin 2009; Europe; Bonanno & Giudice 2010). FQA utilizes 'Conservatism scores' assigned *a priori* to each plant species in region. A species score is based on its sensitivity to anthropogenic disturbance and its likelihood of being found in high-quality remnant natural areas (Taft *et al.* 1997). Simple univariate summaries can then be used to characterize an area's Floristic Quality. Thus, an areas' 'Floristic Quality' refers to the degree to which its plant assemblage is intact and likely to resemble that of a remnant, native habitat, which is dependent on how much anthropogenic degradation the area has accrued and how many of its sensitive Conservative species remain. Floristic Quality metrics have been shown to effectively measure anthropogenic disturbance and site conservation value (Cohen, Carstenn & Lane 2004; Miller & Wardrop 2006; Mack 2007; Mack *et al.* 2008). As only a plant species list is required, the ease of use and novel ecological information captured by FQA has spurred its increasing use in choosing natural areas for acquisition or legal protection. Land managers and researchers commonly also use FQA to determine the effectiveness of management techniques over time (e.g. Brudvig *et al.* 2007; Foster *et al.* 2007). In the United States, legal mandates for habitat monitoring and assessment often require FQA-based criteria (Matthews & Endress 2008; USEPA, 2010). Finally, FQA is increasingly used in basic ecological and conservation research (e.g. Panzer & Schwartz 1998; Spyreas & Matthews 2006; McNicoll & Augspurger 2010).

A key assumption to using FQA is that changes in metric values at a site are orderly and predictable over time. Insufficient understanding of the temporal dynamics of conservation metrics can lead to their misuse (Niemi & McDonald 2004). For example, high plant species richness is often considered indicative of less-disturbed, high conservation value habitats, but this generalization is unwarranted given the inherently non-monotonic trend in richness over time (Fleishman, Noss & Noon 2006). Likewise, high Floristic Quality values are commonly equated with 'mature', 'late', 'advanced', 'climax' or 'stable' successional states (e.g. Swink & Wilhelm 1994; Middleton & Bever 2010), implying that FQA values increase in accordance with successional advance over time. This is not an unreasonable assumption given that rare, specialist or disturbance-sensitive species are often prevalent in or restricted to the oldest or least disturbed habitats (Peterken & Game 1984; Honnay, DeGroote & Hermy 1998; Kindscher & Tieszen 1998; Honnay, Hermy & Coppin 1999). However, if Floristic Quality values do not follow simple, predictable increases during succession as is assumed, their interpretation and use may be confounded.

Studies examining temporal changes in Floristic Quality values after anthropogenic disturbances have not shown consistent results. Time since logging disturbance in mature forests has been shown to correlate with higher Floristic Quality values (Francis *et al.* 2000; Wallace 2001). Chronosequence comparisons typically find older restorations to have higher Floristic Quality values (Mushet, Euliss & Shaffer 2002; Balcombe *et al.* 2005), while studies tracking individual sites often show unexpected deviations from monotonic increases over time (Spieles, Coneybeer & Horn 2006; McIndoe, Rothrock & Reber 2008; Matthews, Spyreas & Endress 2009; Middleton, Bever & Schultz 2010). Decreasing Floristic Quality values in these instances have been concomitant with observations of non-native species invasion, suggesting that non-native species may dictate Floristic Quality values. However, these studies have only observed early-successional (< 20 years) restorations, and the long-term relationship between invasion, succession and Floristic Quality is unexamined. Community invasions that *persist over time* could suspend succession by native plants (Flory & Clay 2010) and/or lead to novel anthropogenic communities (Hobbs *et al.* 2006), thereby dampening native Floristic Quality values. Were non-native invasions to prove persistent, their negative effects on native Floristic Quality would be substantial and widespread (Spyreas *et al.* 2010). Alternately, invasion effects on Floristic Quality may be fleeting and largely limited to early-successional stages if non-native species do not persist.

Even without non-native invasions or other obvious catalysts, developing plant communities can take unpredictable paths towards unexpected states (Hobbs & Norton 1996). Paths towards alternate community types may lead otherwise similar sites to become dissimilar in species compositions over time. However, if Floristic Quality metrics only measure accrued anthropogenic degradation and the time since disturbances, then the stochastic successional processes that produce differing species compositions should not lead to differences in Floristic Quality values. Furthermore, the trajectory of Floristic Quality values over time should not vary among sites that differ in species composition, if the sites have shared anthropogenic disturbance legacies. The temporal predictability of FQA values has not been studied in this way because the restoration sites compared thus far have differed in their anthropogenic disturbances.

We analysed the temporal dynamics of Floristic Quality values in 10 old fields over 50 years of unmanipulated succession after abandonment. If Floristic Quality is inexorably linked to time since anthropogenic disturbance and advancing successional state as is assumed, then Floristic Quality values in these fields will follow a predictable, increasing trajectory during succession. We address four specific predictions:

1. We predict that an asymptotically increasing trajectory will be a better descriptor of temporal trends in Floristic Quality values than either a linear or a peaked model. Previous studies have shown that FQA values in the initial years of wetland restoration commonly exhibit an asymptotically increasing trajectory (Matthews, Spyreas & Endress 2009). Alternatively, a peaked trajectory to Floristic Quality values could arise if FQA values follow species richness over early- to mid-successional timeframes (Anderson 2007) or if fields become increasingly invaded by non-native species (Matthews, Spyreas & Endress 2009). A linearly increasing trajectory could reflect a strong link between Floristic Quality values and advancing successional states, where fields would consistently accumulate Floristic Quality as succession proceeded, and they would not slow or reach an asymptote in values, until rates of species turnover slowed and/or when fields reached successional equilibrium (i.e. as old-growth forest in the present case).

2. We predict that field condition at abandonment (row crop vs. hayfield) will not have long-term effects on Floristic Quality values. Thus, even if there are initial differences in Floristic Quality values associated with abandonment treatments, values will quickly converge on a common trajectory as time since disturbance (i.e. age) becomes the primary Floristic Quality determinant.

3. We predict that Floristic Quality values will exhibit a consistently predictable trajectory regardless of differences in the particular species composition of individual fields. Variation or divergence in FQA values corresponding with variation or divergence in field species compositions would suggest strong controls on FQA values beyond the time since site disturbance (e.g. stochastic successional phenomena) that could limit their utility.

4. While several variants in metric formulations have been proposed for FQA, we predict that the asymptotic FQA trend model will be robust to differences in metric calculations, including those that vary in their spatial sampling scale and those that exclude non-native species.

Materials and methods

The study used data from the Buell-Small Succession Study (BSS) fields, located within the piedmont region of New Jersey, USA (40° 30′ N, 74° 34′ W; http://www.ecostudies.org/bss). The BSS fields were farmed from 1701 to 1958–66, at which time they were abandoned from agriculture and allowed to revegetate without management or manipulation. Fields were abandoned as pairs in alternate years from 1958 to 1966. At abandonment, this parcel was not seen as having been 'farmed out', although the site's soils are characterized as naturally droughty and not very fertile. Since abandonment, the vegetation has been monitored with 48 permanently marked 0·5 × 2·0 m plots within each of 10 fields, from which percentage cover of all species present in plots has been annually or biannually recorded in mid-July to late July. Plots are arranged in a regular pattern that varies slightly with the shape of the field. Most fields abut a nearby old-growth forest preserve. Data collection occurred every year since release, until 1979, when sampling switched to alternate years. The fields also differed in their season of abandonment (autumn or spring), final crop (hayfield or row crops) and soil treatment (ploughed or intact vegetation). 'Season of abandonment' and 'soil treatment' have been found less important than 'final crop' in their effect on succession in the fields (Meiners, Pickett & Cadenasso 2002). Therefore, only the 'final crop' treatment was considered in our study.

Floristic Quality metrics are composed of Coefficients of Conservatism (*C*) previously assigned to New Jersey's flora (BHNP, 2006). Where species sampled in BSS plots were not found in this database, *C* scores were taken from the nearest available state or as the average of the two nearest (e.g. West Virginia, Pennsylvania). Scores range from zero (tolerant of anthropogenic disturbance, no fidelity to remnant habitats) to 10 (Conservative species, intolerant of human stressors, exclusive to remnant habitats) (Taft *et al.* 1997). All non-native species are assigned zeros.

ANALYSIS

To determine which trajectory would best describe trends in Floristic Quality values over time, we used nonlinear least squares regression, using a Gauss–Newton algorithm in SYSTAT 11 to describe Floristic Quality values over time using three models for comparison (Engelman 2005). These models were chosen based on previously demonstrated success at characterizing successional dynamics (Zedler & Callaway 1999; Morgan & Short 2002; Gutrich & Hitzhusen 2004; Anderson 2007; Matthews, Spyreas & Endress 2009). The first model assumed that the value of an FQA metric (Y) increased linearly over time (t):

$$Y(t) = Y_0 + bt \qquad \text{eqn 1}$$

The second model assumed the value of a metric (Y) increased to an asymptote, a trend that is well described by the negative exponential function:

$$Y(t) = Y_0 + a(1 - e^{-bt}) \qquad \text{eqn 2}$$

where t is site age in years, a represents the asymptotic maximum, b is a slope parameter and Y_0 is a y-intercept. Alternatively, values could initially increase to a peak and then decline. Such a trajectory is well described by a double exponential function:

$$Y(t) = Y_0 + a(e^{-ct} - e^{-bt}) \qquad \text{eqn 3}$$

Note that equation 8 reduces to equation 7 if the additional slope parameter c equals zero (i.e. there is no decline from the peak). Support for competing regression models was compared using Akaike Information Criterion, corrected for small sample sizes (AIC_c). We ran analyses using the age of the fields or the year of the sample (i.e. x-axis as field age or calendar year), but these produced similar results so we present data from field ages. The number of fields with data available for analysis varied at any given age (see vertical bars Fig. 1) for two reasons: first, some fields did not have data for the oldest age classes because fields were abandoned in different years (final field ages ranged from 42 to 50) and second, because of the biannual sampling cycle in last half of the study.

We compared effects of field abandonment treatments on Floristic Quality using ANOVA to compare values in the first year and at the final age that had data for all 10 fields. Comparisons at the final age used either 43- or 44-year-old fields because of the biannual sample scheme. Both treatments had equal representation by 43- and 44-year-old fields, the last age that all fields had reached.

Sorensen's distance values were used to represent differences in species composition among fields, as a means of addressing our prediction that Floristic Quality values will exhibit a consistently predictable trajectory regardless of differences in their species composition. Specifically, we used field-level species presence–absences to calculate all pairwise Sorensen's distances among fields for a given year. During transition ages when some fields were being sampled every year and others were already on alternate year sampling schedules, we used all the composition data available, but kept the sample size constant to calculate standard error using the same number of independent comparisons per year (45). Similarly, values only extend to an age of 46 to maintain full sample size for comparisons.

Because various formulations have been proposed for calculating Floristic Quality metrics (Ervin *et al.* 2006; Miller & Wardrop 2006), we examined the robustness of Floristic Quality-time models under

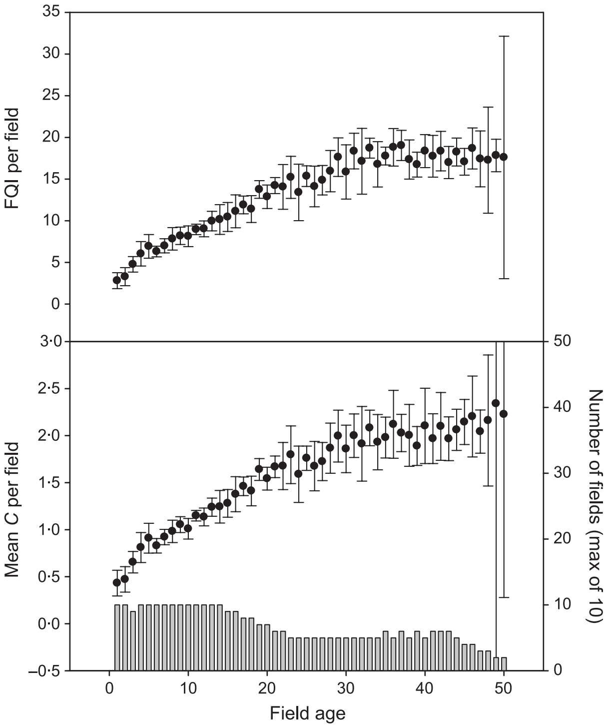

Fig. 1. Trends in Floristic Quality measures in Buell-Small Succession Study fields over time (±95% CI). Sample size for any given age in both graphs is indicated with vertical bars in the lower panel (i.e. right vertical axis), for this and all figures following. Non-native species are included in metric calculations.

different scales of species aggregation and where non-native species were included or excluded from calculations. The first metric compared was Mean C ($\bar{C}$):

$$\overline{C} = \sum C/(S) \qquad \text{eqn 4}$$

where C is the Coefficient of Conservatism values of plant species, and S is the number plant species. Native Mean C ($\bar{C}_{\rm n}$)only considered native species:

$$\bar{C}_{\rm n} = \sum C_{\rm n}/(N) \qquad \text{eqn 5}$$

where $C_{\rm n}$ is the Coefficient of Conservatism values of native plant species and N is the number of native plant species. The Floristic Quality Index (FQI), Floristic Quality Assessment Index (FQAI) and Native Floristic Quality Index ($\text{FQI}_{\rm n}$) were calculated as follows:

$$\text{FQI} = \overline{C} * (\sqrt{S}) \qquad \text{eqn 6}$$

$$\text{FQAI} = \overline{C} * (\sqrt{N}) \qquad \text{eqn 7}$$

$$\text{FQI}_{\rm n} = \overline{C}_{\rm n} * (\sqrt{N}) \qquad \text{eqn 8}$$

With respect to scale, Mean C values were calculated in the following ways. First, 'site'-level values for a given age were calculated from the species list generated from all species encountered in all 480 plots. Second, 'field'-level values were calculated from the accumulated species in the 48 plots in a given field. Finally, 'average-of-plots' values were calculated as the value within plots, averaged across all 48 plots in a field. This third value using plot-level averaging has the effect of emphasizing frequently occurring species. Its calculation was intended to examine suggestions that using plot-level averages may give a more realistic assessment of the Floristic Quality of a field by dampening contributions from outlier, rare or ephemeral species (McIndoe, Rothrock & Reber 2008). This has the same effect as weighting values by their frequency in a community, which has also been suggested for FQA's use (e.g. Francis *et al.* 2000; Cohen, Carstenn & Lane 2004). FQI values could not be compared in instances where sample effort and richness-area effects would bias comparisons (e.g. across years at the site level).

Results

There was no eventual decline in Floristic Quality (Fig. 1, Fig. S1 in Supporting information), effectively reducing equation 8 (peaked function) to equation 7 (asymptotic) (Table 1). Based on this information and AICc, we selected the asymptotic as the more parsimonious model (Table 1). Visual examination of the asymptotic function suggests that Mean C and FQI values are near their maxima 50 years after field abandonment (Fig. S1, Supporting Information). The asymptotic trend was consistent whether or not the metrics included non-native species in their calculation (Table 1), although values without non-native species were higher (Fig. 2). An asymptotic curve was also the best predictor of Mean C across the different scales that species were sampled/aggregated (Fig. 3). Overall species richness in fields declined after a maximum value *c.* 35 years after field abandonment (Fig. 4). Although non-native species richness declined following abandonment (Fig. 4), its trajectory did not vary inversely with FQA values. Non-native species dominance (percentage cover) over time did appear to vary inversely with FQI values. However, the trajectory of non-native dominance did not mirror that of Mean C values over the last ~25 years of the study period.

Abandonment conditions had neither initial nor long-term effects on Floristic Quality (Mean C: Age 1, t = 48; d.f. = 8; P = 0·65; Age 43–44, t = 0·33; d.f. = 8; P = 0·75; FQI, Age 1, t = 0·49; d.f. = 8; P = 0·64; Age 43–44, t = 0·89; d.f = 8; P = 0·4). The only apparent difference in the trajectory of values between abandonment treatments was a more rapid initial rise in row cropfields, approximately between the ages 4–8, after which treatment values quickly converged and showed similar trajectories (Fig. 5; FQI displayed a qualitatively similar pattern and is not shown). Fields varied over time in the number of species they shared, although they generally converged upon an intermediate level of dissimilarity in species composition (Fig. 6). Variation in shared species among fields over time contrasts with variation in FQA values among fields (Fig. 1), which were rather consistent except for a spike in variation at the end of the study period, which was an artefact of the reduction in sample size.

Discussion

The best model for Floristic Quality values over the first 50 years of succession was a negative exponential increase to an asymptote. This trajectory was consistent whether or not non-native species were included in calculations and it was robust to scales of vegetation sampling. Initial field

Table 1. Model comparisons and estimated parameters (Y_0, a, b and c) for Floristic Quality measures. Sample size is 50 in all cases. Results were qualitatively similar for Mean C values calculated at different scales and are not presented

Model	K	AIC_c	ΔAIC	Likelihood	Weight	Y_0	R^2	a	b	c
Mean C										
Negative exponential	3	−103·9	0	1	0·77	0·375	0·975	2·048	−0·044	–
Peaked exponential	4	−101·5	2·367	0·306	0·23	0·375	0·975	2·048	−0·044	0
Linear	2	−76·89	26·96	0·000	0·00	0·767	0·905	–	0·033	–
Mean C_n										
Negative exponential	3	−12·79	0	1	0·77	1·192	0·976	2·588	−0·032	–
Peaked exponential	4	−10·42	2·367	0·306	0·23	1·192	0·976	2·588	−0·032	0
Linear	2	6·285	19·07	0·000	0·00	1·512	0·935	–	0·039	–
FQI										
Negative exponential	3	87·24	0	1	0·77	1·725	0·962	18·57	−0·049	–
Peaked exponential	4	89·61	2·367	0·306	0·23	1·725	0·962	18·57	−0·049	0
Linear	2	112·5	25·27	0·000	0·00	5·902	0·865	–	0·300	–
FQAI										
Negative exponential	3	81·13	0	1	0·77	0·536	0·963	16·24	−0·050	–
Peaked exponential	4	83·49	2·367	0·306	0·23	0·536	0·963	16·24	−0·050	0
Linear	2	106·9	25·77	0·000	0·00	4·242	0·864	–	0·262	–
FQI_n										
Negative exponential	3	94·98	0	1	0·77	3·748	0·957	20·97	−0·047	–
Peaked exponential	4	97·34	2·367	0·306	0·23	3·748	0·957	20·97	−0·047	0
Linear	2	117·4	22·45	0·000	0·00	8·226	0·866	–	0·338	–

FQAI, Floristic Quality Assessment Index; FQI, Floristic Quality Index.

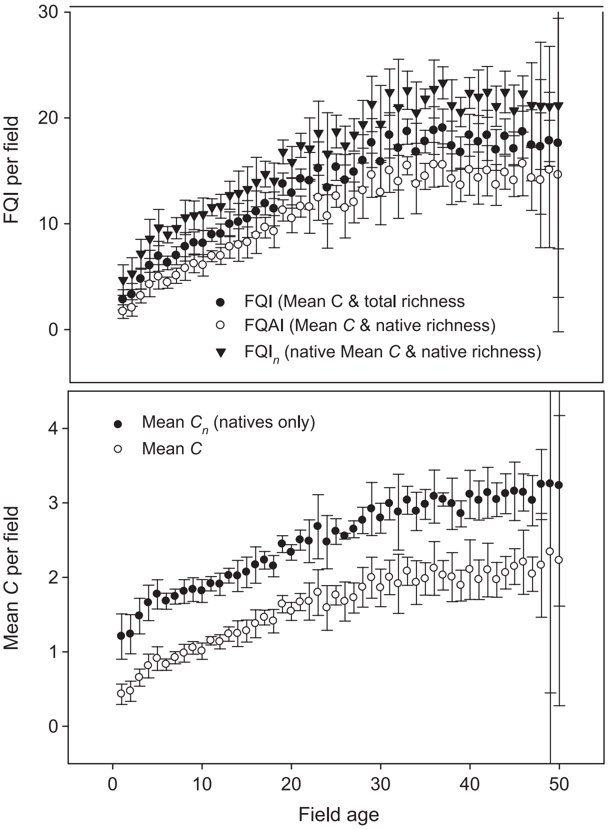

Fig. 2. Trends in Floristic Quality Assessment measures in Buell-Small Succession Study fields over time using calculations that include or exclude non-native species (±95% CI).

condition had some early effects on Floristic Quality values, but trajectories quickly converged among fields and values did not vary between treatments over the long-term. The consistency of FQA value trends despite large temporal variation in species dissimilarity among fields suggests that values are dictated by deterministic successional processes over early- to mid-successional stages.

THE TRAJECTORY OF FLORISTIC QUALITY VALUES OVER TIME

A few studies have reported community-level Floristic Quality values over time. Matthews, Spyreas & Endress (2009) tracked 29 wetland restorations in Illinois for 5–14 years after their creation. Although Floristic Quality values were far more variable among sites and over time compared to those in our study, the majority of their sites were also best described by an asymptotic trajectory model. A similarly shaped logarithmic trajectory best described FQI values in eight Ohio wetland restorations (Gutrich & Hitzhusen 2004), which on average reached an asymptote 8 years after their creation. Finally, values from an Indiana grassland restoration generally increased over 13 years (McIndoe, Rothrock & Reber 2008), although the shape of the trajectory was too erratic to be defined.

While asymptotic trends are most often supported, there appear to be stark differences among studies and systems in the length of time until values plateau. Peaks within 5–10 years typify wetland restorations, whereas at least three decades were necessary in our study's upland fields. Comparatively rapid peaks to Floristic Quality in wetland restorations could have several causes. First, Conservative species are planted in most of these restorations. This is compared to BSS fields, which underwent natural colonization and showed gradually increasing trends. Second, relatively low dispersal limitation and high productivity in wetlands allows for rapid establishment by highly competitive taxa whose dominance then resists new col-

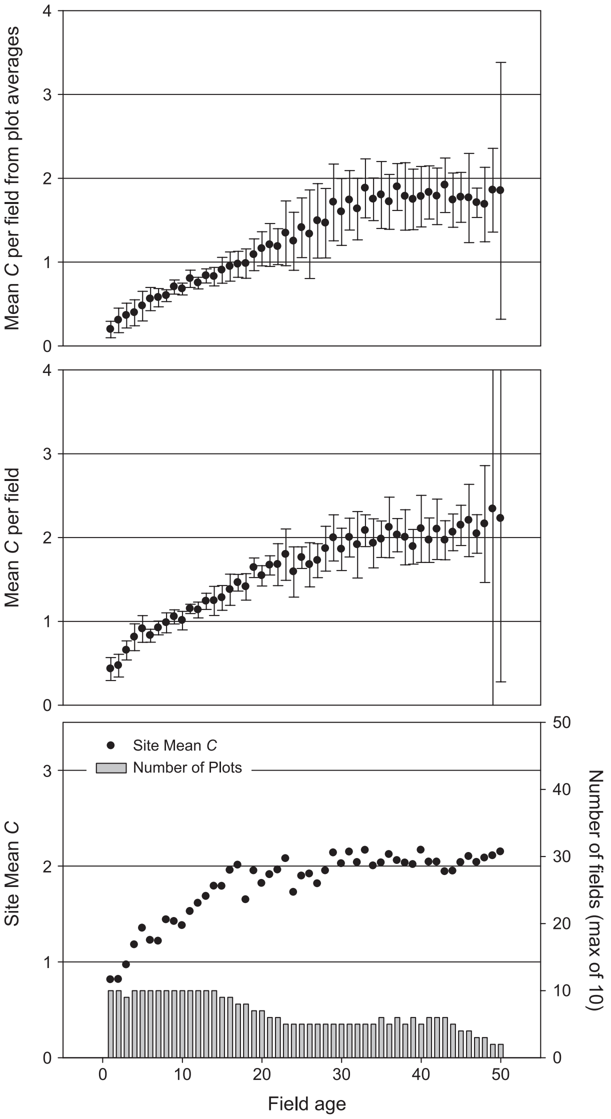

Fig. 3. Mean *C* calculated across sampling spatial scales (the site-level flora, field-level floras and average of plots per field) (±95% CI). Non-native species are included in metric calculations.

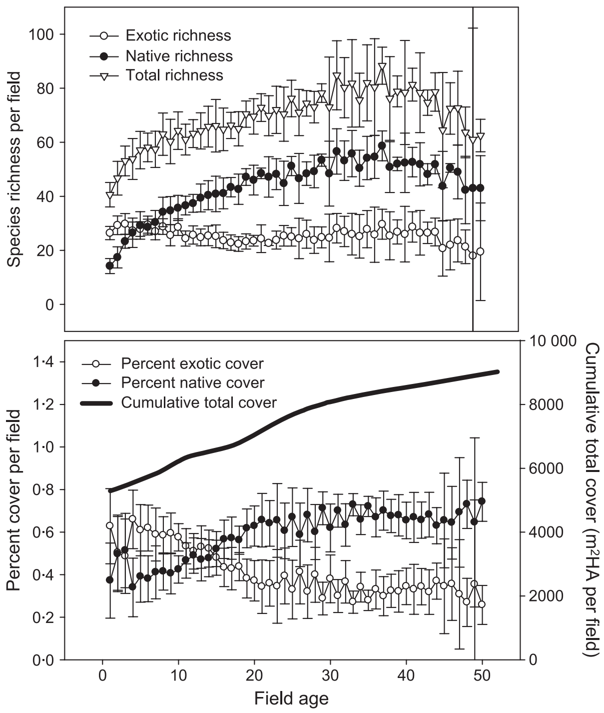

Fig. 4. Trends in non-native and native species in Buell-Small Succession Study fields over time (±95% CI). Percentages are relative contributions to total cumulative cover.

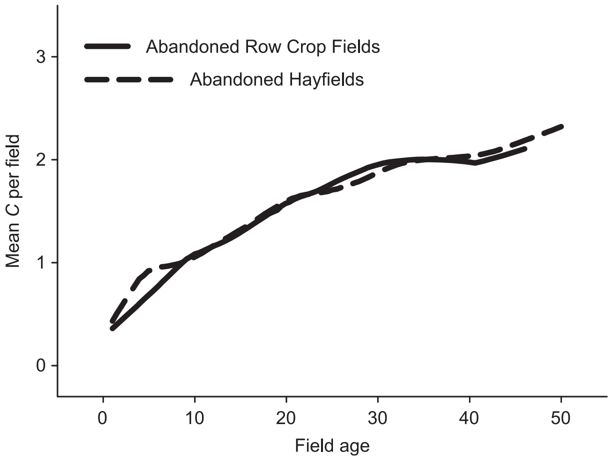

Fig. 5. Trends in Mean *C* values for field abandonment treatments. Non-native species are included in metric calculations. Floristic Quality Index trends were qualitatively similar and are not shown.

onizations (Chen *et al.* 2010). Finally, emergent wetlands could have earlier peaks because their terminal state as a herbaceous community lacks the woody and shade-tolerant forest taxa accompanying the ongoing physiognomic change of BSS fields to forests.

SUCCESSION AND FLORISTIC QUALITY

The Floristic Quality trajectories of BSS fields were notable for their consistent shape (Figs S2–S3, Supporting information) and variation over time (Fig. 1). Additionally, there were no patterns in Floristic Quality values related to year of abandonment or spatial position at the site (data not shown). Therefore, while minor differences in slopes or asymptote values were apparent, no field FQA values took idiosyncratic or divergent paths, suggesting that they were dictated by historical contingency or spatial stochasticity (Vaughn & Young 2010). Similar successional trends to Floristic Quality values may not seem surprising for fields sharing the same species pool and abandoned under similar abiotic conditions (soils, etc.), as this would likely lead to similar species assemblages in fields. However, species dissimilarity among BSS fields was actually quite variable over time, while FQA trends remained consistent. Thus, different species in different fields were producing the same Floristic Quality trends across the site. This is particularly surprising for a metric like FQI, the components of which, species richness and composition, are frequently erratic and

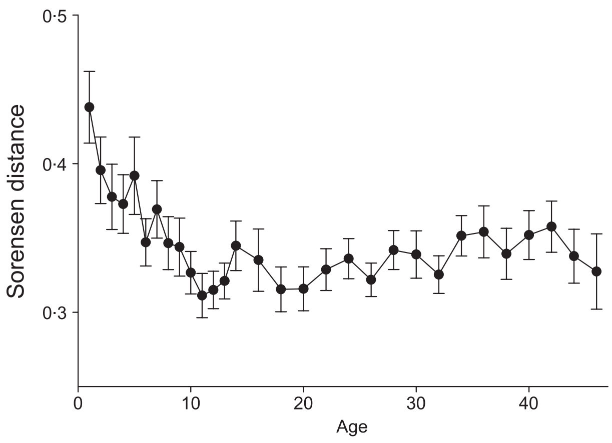

Fig. 6. Dissimilarity in species composition among fields based on Sorensen distance. Data plotted are average compositional distances among all fields at the same age (±95% CI). Analyses switch to alternate years past age 15 reflecting the change in sampling periodicity.

unpredictable during succession (Matthews 1979; Christensen & Peet 1984). Furthermore, initial field conditions (hayfield vs. bare ground) are known to have differentially affected fields in other aspects for 30 years or more after abandonment (e.g. relative representation by annuals and forage grasses, native vs. exotic richness, Meiners, Pickett & Cadenasso 2002), but Floristic Quality values between treatments followed nearly identical trend lines throughout. In total, these results suggest that Floristic Quality was dictated by deterministic processes over time and that FQA measures behave predictably in unmanipulated habitats over early- and mid-successional timeframes.

This finding is also supported by comparing patterns of richness and Floristic Quality in plots vs. fields. While Floristic Quality values had similarly increasing trajectories when calculated per plot, per field or at the site level, species richness behaved differently at different scales. Richness (total and native) per field exhibited distinctly unimodal trends, whereas species richness per individual plot has remained very consistent in BSS plots over time (Meiners, Pickett & Cadenasso 2002). Therefore, species of greater Conservatism replaced less Conservative species in plots, without a net change in species density per plot. However, the same increasing Floristic Quality trends were generated by different increasingly Conservative species in different fields.

On the other hand, species life form was clearly related to successional trends in Floristic Quality values, especially for dominant plants. For example, the first group to dominate was comprised of weedy ephemeral taxa with low *C* values (e.g. *Ambrosia artemisiifolia* L. $C = 0$, *Erigeron annuus* (L.) Pers. $C = 0$), whose populations collapsed within 10 years (Meiners, Rye & Klass 2008). The second group to ascend was comprised of slightly more Conservative perennial herbaceous taxa (e.g. *Aster pilosus* Willd. $C = 1$, *Solidago juncea* Aiton, *S. canadensis* L., *S. gigantea* Aiton, *S. rugosa* Mill. $C = 2$, *Apocynum cannabinum* L. $C = 2$). The third group was made up of the trees, shrubs and woody vines that dominated during later years of the study (e.g. *Acer rubrum* L. $C = 3$, *Rubus allegheniensis* Porter $C = 3$, *Cornus florida* L. $C = 5$, *Vitis* spp. $C = 4$). They first increased Floristic Quality values as they came to dominate communities and then maintained values at their asymptotic levels as old-field herbs declined. However, despite the seeming coupling of life form with species Conservatism levels during succession, life form and Conservatism are not synonymous. Both highly Conservative and non-Conservative species are well represented among all life history, functional group and species trait categories in regional floras. Further study of the yet untested relationship between life form and species Conservatism certainly seems warranted.

A fourth group of species influencing temporal patterns in Floristic Quality values were non-native species, which generally decreased over time in BSS fields relative to natives. Non-natives *directly* decrease Floristic Quality values when included in metric calculations (equations 1, 3 and 4; Fig. 2). However, because there were no differences in the shapes of trajectories for metrics that included or excluded non-natives, non-native presence or richness alone did not determine Floristic Quality value trajectories. Non-native species effects on Floristic Quality values can also occur as an *indirect* function of invader dominance by displacing native species with higher *C* values or by decreasing opportunities for them to establish. Even though several of the most invasive plants in North America (e.g. Rosa multiflora, Microstegium vimineum, Lonicera japonica, Alliaria petiolata, Lonicera maackii; Meiners, Pickett & Cadenasso 2001; Gibson, Spyreas & Benedict 2002; Spyreas *et al.* 2004) are common in BSS fields, decreasing overall non-native dominance may have explained the asymptotic trajectory shape in these fields, rather than the peak-and-decline trajectory sometimes observed for FQA values over time. Therefore, our study does not dispute the majority of evidence that suggests considerable depressive effects on Floristic Quality from strong invasions (e.g. Spyreas *et al.* 2010). As non-native species and their impacts have been suggested as being comparatively minimal in mature forests (Von Holle, Delcourt & Simberloff 2003; Meiners, Rye & Klass 2008; Martin, Canham & Marks 2009), it will be highly informative to follow continued maturation of BSS vegetation with respect to non-native invasions and their effects. Furthermore, because understoreys contain a disproportionate amount of the plant diversity in these forests, future study should consider invasion in different strata and their effects on Floristic Quality in different strata.

Even though BSS fields had become young forests by the end of the study, and despite their adjoining old-growth forest seed source, their understoreys show a glaring absence of Conservative shade-tolerant native forest herbs. Conservative forest herbs were sporadically detected in plots throughout the study period (e.g. *Actea pachypoda* Elliott $C = 5$, *Athyrium felix-feminina* (L.) Roth $C = 7$, *Circaea lutetiana* L. $C = 6$, *Monotropa uniflora* Small $C = 8$, *Phryma leptostachya* L. $C = 8$, *Podophyllum peltatum* L. $C = 6$), but these were singular occurrences that did not persist. The potential for future sustained colonization by these taxa could initiate a second period of increasing Floristic Quality values in BSS fields. However, the notoriously slow migration and establishment by such species into mature forests suggests that this will not occur for hundreds of years, even with adjacent propagule sources (Matlack 1994; Brunet & von Oheimb 1998; Singleton *et al.* 2001; Spyreas & Matthews 2006). Recolonization rates by *Conservative* species in other habitat types have not been directly studied, but long-term comparisons of site histories suggest that if passive recovery by remnant taxa occurs in non-forest habitats, it will be measured over centuries as well (Gibson & Brown 1991; Kirkman *et al.* 2004; Ejrnæs *et al.* 2008). For example, Conservative species are notably absent from grassland restorations even with propagule sources that are directly adjacent (Kindscher & Tieszen 1998; Foster *et al.* 2007).

IMPLICATIONS FOR THE USE OF FLORISTIC QUALITY ASSESSMENT

It could be argued that the increases in Floristic Quality values demonstrated here provide evidence that 'hands-off' approaches to restoration are likely to be successful given enough time; however, we reject this interpretation. Restorations are prone to failure from non-native species invasions (Matthews, Spyreas & Endress 2009). Furthermore, the maximum values in BSS fields (Mean C = 2·25, FQI = 17) were still well below values in remnant habitats with intact floras (e.g. Mean C = 5–6, FQI = 45–55, Swink & Wilhelm 1994), as the highly Conservative species characterizing remnant habitats did not establish. Barring a few exceptional cases (e.g. in North America, Sperry 1994; Gardner 1995), even the oldest restoration projects show considerable deficiencies in their Floristic Quality. Therefore, restoration efforts would do well to focus on Conservative species. In instances where restorations have achieved FQA value parity with remnants, they have received massive planting and management efforts over dozens of years (e.g. repeated overseeding, hand planting of plugs, careful introduction of missing Conservative species, meticulous monitoring, regular prescribed fire, invasive species control).

Three conclusions can be drawn from these results with respect to assumptions underlying FQA's use. First, by illustrating the consistency of Floristic Quality metrics during succession, we demonstrate the robustness of FQA for use across temporal gradients. Second, because these fields reached an asymptote in their FQA values even though they continue to undergo rapid successional turnover (data not shown), temporal changes in FQA values cannot be considered synonymous with succession or with the successional states of communities. Finally, while the relationship between Floristic Quality and time since anthropogenic disturbance may be consistent and predictable, it is not simple (i.e. it is nonlinear). Therefore, FQA users must carefully consider background successional trends in Floristic Quality when using FQA metrics across temporal gradients or for habitats of different ages. For example, Tulbure, Johnston & Auger (2007) concluded that an increase by an invasive species did not decrease a community's Floristic Quality over time. However, the lack of an invasion effect may have been obscured by background increases in Floristic Quality that were likely occurring across the site, which was undergoing rapid succession after a recent disturbance. Similarly, controlling for ambient successional changes in Floristic Quality values in a study of deer browsing effects on the floras of young grassland restorations may have allowed for treatment differences to have been better discerned (Anderson, Dorick & Crispino 2007).

While the asymptotic trajectory model we have described will require further testing for its general applicability in other habitat types, successional stages, regions and landscape settings, we suggest it for use as a baseline expectation for predicting Floristic Quality values over early- to mid-successional timeframes. Deviations from this expected baseline trajectory could highlight relative successes or failures in recovery progress or management practices at sites. Comparative study of site trajectories and their deviations from the expected baseline *en masse* would reveal patterns in the relative importance of specific ecological constraints to the recovery of community-level Floristic Quality.

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Supporting Information

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

Fig. S1. Negative exponential model fit line for FQA measures over time.

Fig. S2. Trends in Mean *C* values over time in individual BSS fields.

Fig. S3. Trends in FQI values over time in individual BSS fields.

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