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Early post-disturbance density trajectories of two co-occurring eupatorieae pioneers, *Ageratum conyzoides* and *Conoclinium coelestinum*, in a single burnt-and-cleared plot in Southern Nigeria

O. E. Michael*, O. M. Agbogidi, A. H. Erhenhi

Department of Botany, Faculty of Science, Delta State University, Abraka, Nigeria

Key words: Early post-disturbance recolonization, Secondary succession, Pioneer speciesp, Eupatorieae, Colonization rate index, Tropical agroecosystem, Bush-fallow

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ABSTRACT

Early recolonization after fire and clearing is commonly attributed to pioneer species, but time-resolved comparisons of how co-occurring pioneers perform under the same disturbance remain limited. We compared post-disturbance density trajectories of *Ageratum conyzoides* L. and *Conoclinium coelestinum* (L.) DC. (Asteraceae: Eupatorieae) in a single 100 m² plot at a humid tropical lowland site in Abraka, southern Nigeria, that was burnt and hand-cleared. Five 4 m² quadrats (20 m² in total) were censused at Weeks 2, 4, 6, 8, 10 and 12 of monitoring (n = 3 replicates per species per date), and the vegetation was analysed as two focal-species-centred assemblages (Assemblage A, *A. conyzoides* plus six associates; Assemblage B, *C. coelestinum* plus six associates) drawn from the same quadrats. The disturbance was not replicated, so quadrats and readings are repeated samples within one event rather than replicates of the disturbance. Both focal species were recorded at the first census (mean density 0.67 each). Likelihood-ratio mixed-effects models showed that density differed among species (χ^2 = 128.82 and 58.34, df = 6, $p < 0.001$) and across weeks (χ^2 = 28.54, $p < 0.001$; χ^2 = 15.61, p = 0.008) in Assemblages A and B, respectively, but Species × Week interactions were not significant (p = 0.697 and 0.822), and neither focal species showed significant within-species change across weeks (p = 0.4651 and 0.4360). Descriptively, *A. conyzoides* rose from 0.67 to 1.00 (Colonization Rate Index, CRI, +49.3%; relative density 8.36% to 7.90%), whereas *C. coelestinum* rose from 0.67 to 2.67 (CRI +298.5%, the highest of the 14 species; relative density 6.92% to 17.42%), and principal component analysis (PC1 = 79.8% and 65.7%) and Ward's hierarchical cluster analysis placed it with the actively expanding species; evenness was high (J′ = 0.886–0.973). Within this single disturbance event, both species were therefore present from the first census and their observed net density change differed, with a markedly larger increase in *C. coelestinum*, but the formal test did not detect a statistically significant differential temporal response, and the contrast rests on descriptive evidence from low counts (all mean densities ≤ 3.33). The findings are hypothesis-generating and require replicated disturbance events for confirmation.

***Corresponding Author:** O. E. Michael ✉ meozioma@delsu.edu.ng

INTRODUCTION

Fire and mechanical clearing are among the most widespread disturbances in tropical agroecosystems, where shifting cultivation and bush-fallow practice repeatedly expose bare ground to recolonization (Pickett and White, 1985; Uhl, 1987). In classical models of secondary succession, early colonizers pre-empt freed resources before they are supplemented or replaced by competitively superior taxa (Connell and Slatyer, 1977; Bazzaz, 1979; Guariguata and Ostertag, 2001). Which species recolonize first, and how their abundances change over the following weeks, therefore shapes the starting point of recovery.

'Pioneer' is nevertheless a coarse label. Pioneers are generally characterized by rapid germination, high reproductive output and fast growth (Grime, 1977), and Asteraceae contribute heavily to the pioneer flora of disturbed tropical land (Kohli *et al.*, 2006; Batish *et al.*, 2009). Yet co-occurring pioneers can differ in life history, and differences in niche and fitness among co-occurring species are central to current accounts of community assembly (HilleRisLambers *et al.*, 2012). Disturbance also releases resources in a pulse (Hobbs and Huenneke, 1992; Davis *et al.*, 2000), so species that share a label may differ in how long they keep gaining density once the pulse is being taken up. Whether a shared functional label predicts shared early trajectories is an empirical question that needs repeated, species-level counts under a common disturbance.

Ageratum conyzoides L. is an annual herb of American origin, now pantropical, that is reported as an early colonizer of abandoned fields and shifting-cultivation sites; it combines prolific seed production with vegetative reproduction and produces allelochemicals (Kohli *et al.*, 2006; Batish *et al.*, 2009; Kaur *et al.*, 2023). *Conoclinium coelestinum* (L.) DC. is a rhizomatous perennial of the same tribe (Eupatorieae) with a strongly similar blue-violet capitulum and capacity for lateral vegetative spread. The two are morphologically similar, co-occur on disturbed ground at our site, and are both routinely called early colonizers (voucher specimens DELSUH-309 and DELSUH-269, Delta State University Herbarium). They differ, however, in life form (annual versus rhizomatous perennial). Comparing them under one disturbance regime and one sampling scheme therefore offers a controlled contrast in life history while holding site, disturbance and timing constant. Quantitative, time-resolved comparisons of these two species appear scarce in the sources we consulted; we make no claim of priority, and we frame the study as a descriptive case study of one disturbance event.

We asked: after an identical burn-and-clear disturbance, do *A. conyzoides* and *C. coelestinum* follow similar or different density trajectories over the first 12 weeks of monitoring, and how do those trajectories sit within the structure of their co-occurring assemblages? We evaluated three hypotheses, each with a stated evidential basis:

H1: *C. coelestinum* shows a greater net increase in density between Week 2 and Week 12 than *A. conyzoides* (evaluated descriptively by CRI and relative density, and by assemblage-level multivariate position).
H2: The two species follow divergent temporal trajectories despite shared early presence (the only formal test of this is the Species × Week interaction in the mixed-effects models; PCA, HCA and CRI are descriptive).
H3: Differences between the focal species are reflected in their position relative to co-occurring associates (PCA and HCA, descriptive).

Because the disturbance was applied once, we do not test whether these patterns recur across independent disturbance events.

MATERIALS AND METHODS

Study site

The study was conducted at Site III of the Botanical Garden of the Department of Botany, Delta State University, Abraka, Delta State, Nigeria (5.7894° N, 6.1023° E), a humid tropical lowland site with a bimodal rainfall regime within a derived-

savanna/secondary-forest mosaic typical of bush-fallow landscapes of southern Nigeria.

Disturbance, plot and experimental unit

A single 100 m² plot (10 m × 10 m) was demarcated with tape, pegs and rope, and five 4 m² quadrats (20 m² in total) were marked within it (Fig. 1). Existing vegetation was burnt and then cleared by hand to approximate the bush-clearing-and-burning regime of local shifting cultivation (Agbogidi and Ofuoku, 2009; Erhenhi and Obadoni, 2016). Recolonizing vegetation recorded in these quadrats was organized into two focal-species-centred assemblages: Assemblage A (*A. conyzoides* and six associates: *Panicum maximum* Jacq., *Tridax procumbens* L., *Cleome rutidosperma* DC., *Aspilia africana* (Pers.) C.D.Adams, *Celosia leptostachya* Benth., *Asystasia gangetica* (L.) T.Anderson) and Assemblage B (*C. coelestinum* and six associates: *Sacciolepis africana* C.E.Hubb. and Snowden, *Cynodon dactylon* (L.) Pers., *Cyathula prostrata* (L.) Blume, *Gomphrena serrata* L., *Amaranthus spinosus* L., *Trianthema portulacastrum* L.). Associates were the species most frequently co-occurring with each focal species. The two assemblages are alternative groupings of counts from the same quadrats and the same disturbance event; they are not independent communities.

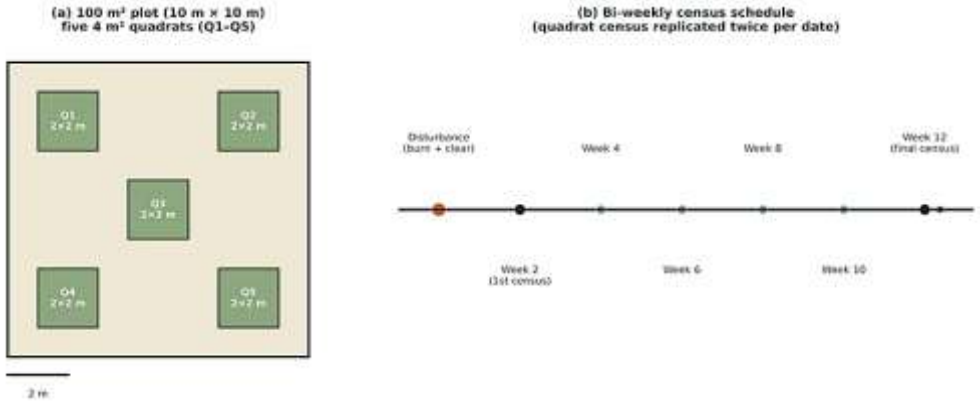


Fig. 1. Layout of the single 100 m² disturbed plot, showing the five 4 m² quadrats (repeated sampling units shared by both assemblages) and the census schedule (Weeks 2–12)
The disturbance was applied once and was not replicated.

Experimental unit and inferential scope

The disturbance event is the experimental unit, and it was not replicated. The five quadrats and repeated censuses provide repeated sampling of one event; they are not independent replicates of the disturbance. All inferential statistics below therefore describe patterns within this event and do not test whether they would recur in other disturbance events or sites (Hurlbert, 1984).

Census and density

Sampling began three weeks after disturbance, once recolonizing vegetation was sufficiently established for reliable enumeration, and the five quadrats were censused at two-week intervals (Weeks 2, 4, 6, 8, 10 and 12 of the monitoring sequence), giving n= 3 replicates per species per date. Population density was calculated as the total number of individuals recorded in the quadrats divided by the number of quadrats studied, so it is expressed as the mean number of individuals per quadrat (4 m² sampling area), not per unit ground area.

Relative density (%) was the density of a species divided by the summed density of all species in its assemblage, multiplied by 100 (Mueller-Dombois and Ellenberg, 1974; Smith and Smith, 2001). Density and relative density are distinct quantities.

Assemblage diversity

Shannon–Wiener H′ (Shannon, 1948), Simpson 1–D (Simpson, 1949) and Pielou's J′ (Pielou, 1966) were

calculated for each assemblage and week from weekly mean densities: $H' = -\Sigma\, p_i \ln p_i$; $1-D = 1 - \Sigma\, p_i^2$; $J' = H'/\ln S$, where p_i is the proportional mean density of species *i*. Richness was fixed at S = 7 in both assemblages by construction (Section 2.2), so the indices describe evenness among the seven selected species rather than the diversity of the whole community.

Inferential statistics

Changes in density across weeks (Weeks 2–12) within each species were tested by repeated-measures ANOVA, with the readings from the quadrats treated as the repeated measures, and differences among species within each week by one-way ANOVA; both were run in SPSS.

For each assemblage separately, a linear mixed-effects model with Species and Week (categorical) and their interaction as fixed effects and quadrat as a random intercept, to account for repeated measurements within quadrats, was fitted to density, and each term was tested by a likelihood-ratio χ^2 test (df = 6, 5 and 30, respectively). Because quadrats and readings are repeated samples within one disturbance event, all P values are interpreted as describing this event only. Permutational multivariate tests (for example PERMANOVA) and formal indicator-species analysis were not performed because they require independent plot-level replication that the design lacks.

Multivariate analyses (descriptive)

PCA was performed on each assemblage's standardized (z-scored) matrix of six weekly mean densities × seven species, with weeks as observations and species as variables, to describe a dominant axis of density change (PC1) and a secondary axis (PC2). With six observations and seven variables, PCA is used only to summarize structure; coefficients in Table 5 are eigenvector coefficients. Hierarchical cluster analysis used Ward's linkage (Ward, 1963) on Euclidean distances between species, calculated from weekly mean densities standardized (z-scored) within each sampling week across the seven species of the assemblage (StandardScaler default), cut at k = 3, with the cophenetic correlation coefficient as a measure of dendrogram fidelity. Because standardization was applied within weeks across species, groups reflect each species' relative density position in the assemblage through time (amplitude) as much as the temporal shape of its trajectory. Both analyses were run in Python (scikit-learn, SciPy) and are interpreted as consistent with, not as evidence for, particular processes.

Colonization rate index (descriptive)

CRI (%) = [(density at Week 12 – density at Week 2) / density at Week 2] × 100. CRI is an author-defined descriptive summary with no sampling distribution or significance test, computed from the tabulated (two-decimal) weekly means. Because it is proportional, it is sensitive to very small starting densities, so the absolute change in mean density (Δ) is reported beside it.

RESULTS

Density and relative density of the focal species

Both focal species were recorded at the first census, at the same mean density (0.67; Tables 1–2; Fig. 2a,b). *A. conyzoides* varied between 0.67 and 1.00 across weeks (relative density 7.50–8.58%; 8.36% at Week 2 and 7.90% at Week 12) with no significant change across weeks (p = 0.4651; Table 1). *C. coelestinum* rose from 0.67 at Week 2 to 2.67 at Week 12 without ever declining (0.67, 1.33, 1.67, 2.00, 2.00, 2.67), and its relative density rose from 6.92% to 17.42%, a 2.5-fold increase (Table 2). Within-species change across weeks was nevertheless not significant for *C. coelestinum* (p = 0.4360). At Week 12 its relative density equalled that of *Cyathula prostrata* (17.42%) and was exceeded only by *Sacciolepis africana* (21.72%).

Among associates, significant change across weeks ($p < 0.05$) occurred in Assemblage A for *Tridax procumbens*, *Cleome rutidosperma*, *Celosia leptostachya* and *Asystasia gangetica*, and in

Assemblage B for *Cyathula prostrata*, *Amaranthus spinosus* and *Trianthema portulacastrum*. Differences among species were significant in five of six weeks in Assemblage A (all but Week 4, p = 0.0508) and in none of the weeks in Assemblage B (p = 0.1202–0.4153). The grasses (*Panicum maximum*, *Sacciolepis africana*) had the highest densities in both assemblages (2.67–3.33 individuals).

Table 1. Population density (mean ± SD, individuals per quadrat; relative density, %, in parentheses) by week in the *Ageratum*-centred assemblage (Assemblage A), with P values across weeks within species (repeated-measures ANOVA) and across species within weeks (one-way ANOVA)

Species	Week 2	Week 4	Week 6	Week 8	Week 10	Week 12	P (weeks)
Panicum maximum	2.67 ± 0.58 (33.33)	3.00 ± 0.00 (25.73)	3.00 ± 0.00 (34.60)	3.33 ± 0.58 (24.98)	3.33 ± 0.58 (26.30)	3.33 ± 0.58 (26.30)	0.1969
Tridax procumbens	0.33 ± 0.58 (4.12)	1.00 ± 1.00 (8.58)	0.33 ± 0.58 (3.81)	1.00 ± 1.00 (7.50)	1.00 ± 1.00 (7.90)	1.00 ± 1.00 (7.90)	0.0297
Cleome rutidosperma	1.67 ± 0.58 (20.85)	2.00 ± 1.00 (17.15)	2.00 ± 1.00 (23.07)	2.67 ± 0.58 (20.03)	2.67 ± 0.58 (21.09)	2.67 ± 0.58 (21.09)	0.0167
Ageratum conyzoides (F)	0.67 ± 0.58 (8.36)	1.00 ± 1.00 (8.58)	0.67 ± 0.58 (7.73)	1.00 ± 1.00 (7.50)	1.00 ± 1.00 (7.90)	1.00 ± 1.00 (7.90)	0.4651
Aspilia africana	1.00 ± 0.00 (12.48)	1.33 ± 0.58 (11.41)	1.00 ± 0.00 (11.53)	1.33 ± 0.58 (9.98)	1.33 ± 0.58 (10.51)	1.33 ± 0.58 (10.51)	0.4651
Celosia leptostachya	0.67 ± 0.58 (8.36)	2.33 ± 0.58 (19.98)	0.67 ± 0.58 (7.73)	2.33 ± 0.58 (17.48)	2.33 ± 0.58 (18.40)	2.33 ± 0.58 (18.40)	<0.0001
Asystasia gangetica	1.00 ± 1.00 (12.48)	1.00 ± 1.00 (8.58)	1.00 ± 1.00 (11.53)	1.67 ± 1.53 (12.53)	1.00 ± 1.00 (7.90)	1.00 ± 1.00 (7.90)	0.0297
P (species)	0.0067	0.0508	0.0025	0.0432	0.0099	0.0099	—

Data are repeated samples (n = 3 replicates per cell) from five 4 m² quadrats in one disturbed plot. F, focal species.

Table 2. As Table 1, for the *Conoclinium*-centred assemblage (Assemblage B)

Species	Week 2	Week 4	Week 6	Week 8	Week 10	Week 12	P (weeks)
Sacciolepis africana	2.67 ± 0.58 (27.58)	3.00 ± 0.00 (23.70)	3.00 ± 0.00 (28.12)	3.33 ± 0.58 (22.20)	3.33 ± 0.58 (22.71)	3.33 ± 0.58 (21.72)	0.1969
Cynodon dactylon	1.67 ± 1.53 (17.25)	1.00 ± 1.00 (7.90)	0.33 ± 0.58 (3.09)	1.00 ± 1.00 (6.67)	1.00 ± 1.00 (6.82)	1.00 ± 1.00 (6.52)	0.5972
Cyathula prostrata	1.67 ± 0.58 (17.25)	2.00 ± 1.00 (15.80)	2.00 ± 1.00 (18.74)	2.67 ± 0.58 (17.80)	2.67 ± 0.58 (18.21)	2.67 ± 0.58 (17.42)	0.0167
Conoclinium coelestinum (F)	0.67 ± 0.58 (6.92)	1.33 ± 0.58 (10.51)	1.67 ± 0.58 (15.65)	2.00 ± 1.00 (13.33)	2.00 ± 1.00 (13.64)	2.67 ± 0.58 (17.42)	0.4360
Gomphrena serrata	1.33 ± 0.58 (13.74)	2.00 ± 1.73 (15.80)	2.00 ± 1.73 (18.74)	2.00 ± 1.73 (13.33)	2.33 ± 2.31 (15.89)	2.33 ± 2.31 (15.20)	0.8289
Amaranthus spinosus	0.67 ± 0.58 (6.92)	2.33 ± 0.58 (18.40)	0.67 ± 0.58 (6.28)	2.33 ± 0.58 (15.53)	2.33 ± 0.58 (15.89)	2.33 ± 0.58 (15.20)	<0.0001
Trianthema portulacastrum	1.00 ± 1.00 (10.33)	1.00 ± 1.00 (7.90)	1.00 ± 1.00 (9.37)	1.67 ± 1.53 (11.13)	1.00 ± 1.00 (6.82)	1.00 ± 1.00 (6.52)	0.0297
P (species)	0.1202	0.1857	0.4153	0.2865	0.2078	0.1565	—

F, focal species

Mixed-effects models

Species had a strong effect on density in both assemblages (A: $\chi^2 = 128.82$, df = 6, $p < 0.001$; B: $\chi^2 = 58.34$, df = 6, $p < 0.001$), and Week had a smaller but significant effect (A: $\chi^2 = 28.54$, df = 5, $p < 0.001$; B: $\chi^2 = 15.61$, df = 5, p = 0.008). The Species × Week interaction was not significant in either assemblage (A: $\chi^2 = 25.56$, df = 30, p = 0.697; B: $\chi^2 = 22.84$, df = 30, p = 0.822; Table 3). The data therefore provide no statistical evidence, in this event, that species differed in how their density changed over time.

Assemblage diversity

Evenness was high in both assemblages (J′ = 0.886–0.973; Table 4). Shannon–Wiener H′ ranged from 1.724 (Week 6) to 1.853 (Week 4) in Assemblage A and from 1.778 (Week 6) to 1.893 (Week 8) in Assemblage B; Simpson 1–D ranged from 0.787 to 0.843. Both assemblages had their lowest H′ at Week 6.

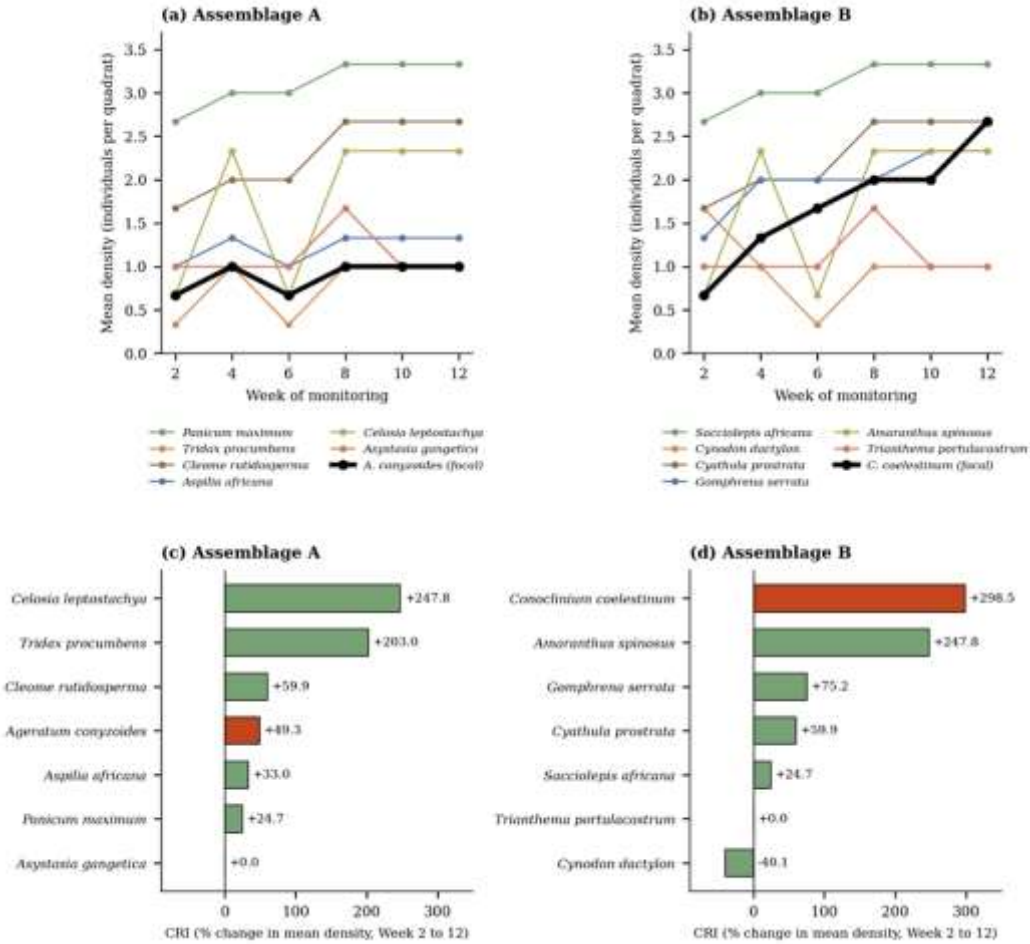


Fig. 2. Density trajectories and colonization rate index (CRI)

(a, b) Mean population density (n = 3 replicates; individuals per quadrat) by week of monitoring in Assemblage A and Assemblage B; the focal species is the bold black line and associates are coloured lines. (c, d) CRI (% change in mean density, Week 2 to Week 12) by species; the focal species is shown in terracotta. All panels are descriptive; the Species × Week interaction was not significant (Table 3).

Table 3. Likelihood-ratio mixed-effects models for the effects of species, week and species × week on population density in each assemblage

Assemblage	Effect	df	χ^2	p	Reading
A	Species	6	128.82	< 0.001	Densities differ among species
A	Week	5	28.54	< 0.001	Density changes across weeks
A	Species × Week	30	25.56	0.697	No differential temporal response detected
B	Species	6	58.34	< 0.001	Densities differ among species
B	Week	5	15.61	0.008	Density changes across weeks
B	Species × Week	30	22.84	0.822	No differential temporal response detected

Quadrat was included as a random intercept. Quadrats and readings are repeated samples within one disturbance event, so tests describe this event only.

Principal component analysis

In Assemblage A, PC1 explained 79.8% and PC2 12.9% of variance (Fig. 3a; Table 5). PC1 ordered the weeks along a gradient of increasing density, separating the lower-density Weeks 2 and 6 from Weeks 8, 10 and 12; PC2 was dominated by *Asystasia gangetica* (coefficient 0.904). *Tridax procumbens*, *A. conyzoides*, *Aspilia africana* and *Celosia leptostachya* had numerically identical coefficients (PC1 = 0.412, PC2 = −0.177), meaning that their

standardized weekly trajectories are the same. In Assemblage B, PC1 explained 65.7% and PC2 18.1% (Fig. 3b); Week 2 lay at the negative extreme of PC1 and Weeks 8–12 at the positive extreme. PC2 separated *Cynodon dactylon* and *Trianthema portulacastrum* (coefficients 0.631 and 0.612) from the remaining species. The vector of *C. coelestinum* (PC1 = 0.437, PC2 = −0.135) was distinct from, but aligned with, those of *Cyathula prostrata*, *Gomphrena serrata* and *Amaranthus spinosus*.

Table 4. Assemblage-level diversity by week, calculated from weekly mean densities (Tables 1–2)

Week	A: H′	A: 1–D	A: J′	B: H′	B: 1–D	B: J′
2	1.759	0.799	0.904	1.838	0.825	0.945
4	1.853	0.829	0.952	1.873	0.837	0.963
6	1.724	0.787	0.886	1.778	0.812	0.914
8	1.852	0.830	0.952	1.893	0.843	0.973
10	1.829	0.823	0.940	1.870	0.837	0.961
12	1.829	0.823	0.940	1.869	0.837	0.961

Species richness was S = 7 in every case by construction, so indices describe evenness among the seven selected species. H′, Shannon–Wiener index (nats); 1–D, Simpson's index; J′, Pielou's evenness.

Table 5. Species-level descriptive summary

Assemblage	Species	PC1	PC2	HCA group	Density Wk 2 → Wk 12	Δ	CRI (%)
A	*Celosia leptostachya*	0.412	−0.177	Actively expanding	0.67 → 2.33	+1.66	+247.8
A	*Tridax procumbens*	0.412	−0.177	Low-density background	0.33 → 1.00	+0.67	+203.0
A	*Cleome rutidosperma*	0.378	0.189	Actively expanding	1.67 → 2.67	+1.00	+59.9
A	*Ageratum conyzoides* (F)	0.412	−0.177	Low-density background	0.67 → 1.00	+0.33	+49.3
A	*Aspilia africana*	0.412	−0.177	Low-density background	1.00 → 1.33	+0.33	+33.0
A	*Panicum maximum*	0.381	0.147	Dominant grass	2.67 → 3.33	+0.66	+24.7
A	*Asystasia gangetica*	0.182	0.904	Low-density background	1.00 → 1.00	0.00	0.0
B	*Conoclinium coelestinum* (F)	0.437	−0.135	Actively expanding	0.67 → 2.67	+2.00	+298.5
B	*Amaranthus spinosus*	0.374	0.300	Actively expanding	0.67 → 2.33	+1.66	+247.8
B	*Gomphrena serrata*	0.432	−0.294	Actively expanding	1.33 → 2.33	+1.00	+75.2
B	*Cyathula prostrata*	0.447	0.169	Actively expanding	1.67 → 2.67	+1.00	+59.9
B	*Sacciolepis africana*	0.463	0.062	Dominant grass	2.67 → 3.33	+0.66	+24.7
B	*Trianthema portulacastrum*	0.162	0.612	Low-density background	1.00 → 1.00	0.00	0.0
B	Cynodon dactylon	−0.205	0.631	Low-density background	1.67 → 1.00	−0.67	−40.1

PCA eigenvector coefficients (PC1, PC2), Ward's HCA group (k = 3), mean density at Weeks 2 and 12, absolute change (Δ, from tabulated means) and Colonization Rate Index (CRI, % change Week 2 to Week 12). All columns are descriptive; none is a significance-tested quantity. Species with identical weekly mean series have identical coefficients. Rows are ordered by CRI within assemblage. F, focal species.

Hierarchical cluster analysis

Ward's HCA resolved three groups in each assemblage (Fig. 3c,d; Table 5; cophenetic r = 0.768 and 0.712 for Assemblages A and B). In both, one dominant grass (*P. maximum*; *S. africana*) formed an outlying group. A low-density background group comprised *Tridax procumbens*, *A. conyzoides*, *Aspilia africana* and *Asystasia gangetica* in Assemblage A and *Cynodon dactylon* and *Trianthema portulacastrum* in Assemblage B. The actively expanding group comprised *Cleome rutidosperma* and *Celosia leptostachya* in Assemblage A, and *C. coelestinum*, *Cyathula prostrata*, *Gomphrena serrata* and *Amaranthus spinosus* in Assemblage B.

Colonization rate index

C. coelestinum had the highest CRI of the 14 species (+298.5%; Δ = +2.00), above *Amaranthus spinosus* (+247.8%; Δ = +1.66) and *Celosia leptostachya* (+247.8%; Δ = +1.66; Table 5; Fig. 2c). *A. conyzoides* had a CRI of +49.3% (Δ = +0.33), ranking fourth of seven in Assemblage A, below *Celosia leptostachya* (+247.8%), *Tridax procumbens* (+203.0%) and *Cleome rutidosperma* (+59.9%). *Cynodon dactylon* declined (−40.1%).

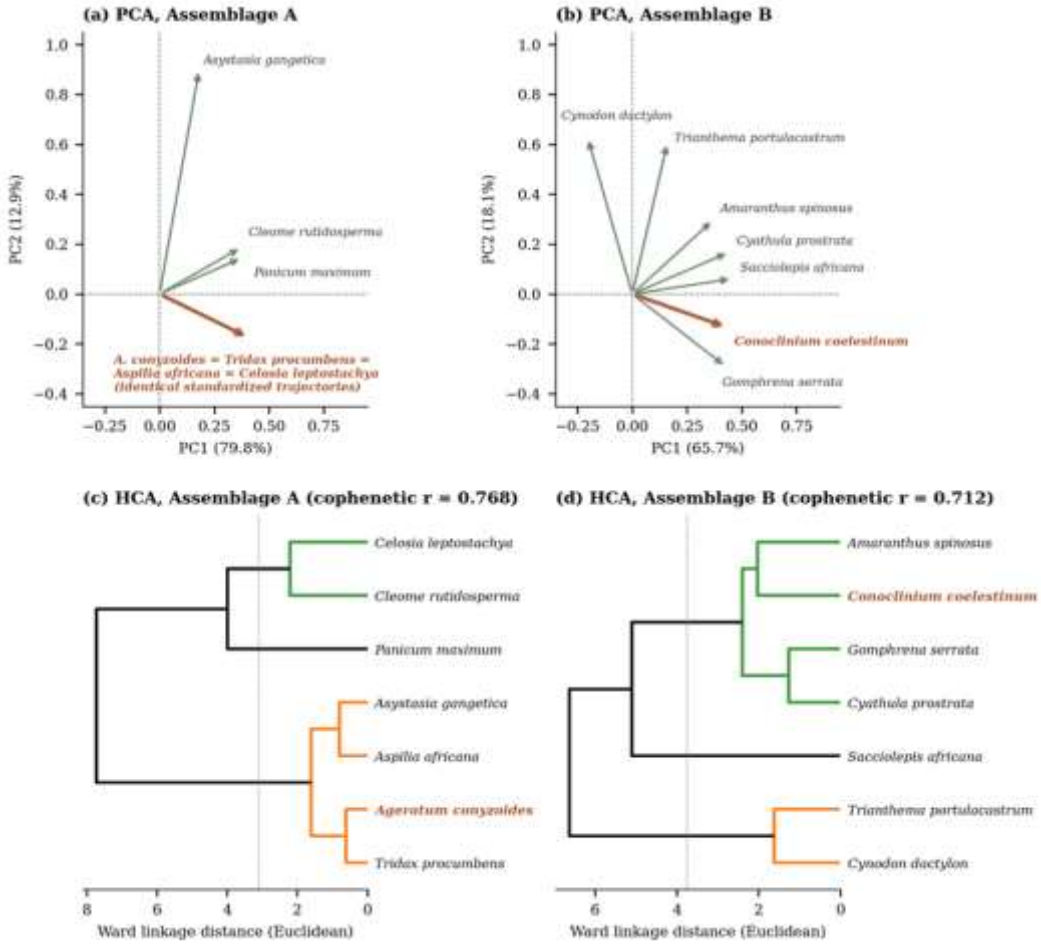


Fig. 3. Descriptive multivariate summaries of the two assemblages

(a, b) PCA biplots of standardized weekly mean densities (axes, PC1 and PC2 with percentage of variance explained; terracotta arrow, focal species; green arrows, associates). In Assemblage A, *A. conyzoides*, *Tridax procumbens*, *Aspilia africana* and *Celosia leptostachya* have identical coefficients and therefore overlap. (c, d) Ward's-linkage dendrograms (Euclidean distance on mean densities standardized within each week across species; coloured branches, the k = 3 groups; terracotta label, focal species). These are descriptive and not significance-tested; weeks are observations, so n = 6 per assemblage.

DISCUSSION

Evidence for a difference in early density trajectories

We asked whether two co-occurring pioneers that share a functional label also share an early density trajectory. Both species were recorded together at the first census at an identical mean density, and thereafter their observed net change differed. *A. conyzoides* changed little (0.67 to 1.00), whereas *C. coelestinum* rose from 0.67 to 2.67 and increased about 2.5-fold in relative density.

The one test that directly addresses whether trajectories differ, the Species × Week interaction, did not detect a differential temporal response in either assemblage (p = 0.697 and 0.822). Neither focal

species changed significantly across weeks on its own ($p = 0.4651$ and 0.4360). The divergence is therefore best described as an observed, descriptive difference within this plot. It is supported by CRI, relative density, PCA and HCA, but it is not a statistically established divergent response.

A non-significant interaction is not evidence of parallel trajectories. With 42 species × week cells, only three replicates per cell and low counts (every mean density ≤ 3.33), the interaction test probably has limited power, although no power analysis can be made from the available data. Conversely, the descriptive methods are not independent confirmations of one another, because they derive from the same weekly means and so share the same small counts.

Shared early presence after disturbance

That both species were recorded from the first census, at the same density, is consistent with reports of both as early colonizers of cleared and abandoned land (Kohli *et al.*, 2006; Kaur *et al.*, 2023). It also fits the general view that resource pulses released by disturbance are rapidly exploited by colonizing plants (Hobbs and Huenneke, 1992; Davis *et al.*, 2000). Davis *et al.* (2000) propose a general theory in which invasibility increases as unused resources accumulate, so the link to this disturbance is conceptual. The design cannot go further. There was no unburnt reference, no pre-disturbance survey and no seed-bank or propagule-source data, and the first census came after disturbance. We therefore cannot say how or when each species arrived, or that its presence depended on the disturbance.

Contrasting density trajectories

In relative terms, *A. conyzoides* held a nearly constant share of Assemblage A (7.50–8.58%). By contrast, *C. coelestinum* progressively gained share in Assemblage B and, by Week 12, matched *Cyathula prostrata* and trailed only *Sacciolepis africana*. Its rise was graded across weeks, in contrast to the alternating pattern seen in *Celosia leptostachya*, *Amaranthus spinosus* and *Tridax procumbens*, which were low at Weeks 2 and 6 and high at Weeks 4 and 8–12. Its CRI and absolute change (+298.5%; Δ = +2.00) were the largest of the 14 species, although only modestly above *Amaranthus spinosus* (Δ = +1.66). These contrasts should be read at the scale of the data. The *A. conyzoides* CRI of +49.3% corresponds to a change of +0.33 in mean density, and CRI values are inflated by very low starting densities. The synchronous low values of several species at Weeks 2 and 6, and the lowest H′ at Week 6 in both assemblages, are not explained by the present data and are not interpreted ecologically.

Assemblage structure and diversity

Evenness was high ($J' = 0.886–0.973$), indicating that abundance was not concentrated in a single species. The grasses *Panicum maximum* and *Sacciolepis africana* held the largest shares, reaching 34.60% and 28.12% relative density. Richness was fixed at seven by design, so this is evenness among the selected species and is not evidence about the diversity of the recovering vegetation as a whole, whose other species were not analysed. The multivariate results are descriptive. PC1 largely tracks overall density change through time in both assemblages, so it represents a shared temporal gradient and not a species contrast. *C. coelestinum* aligned with, and clustered among, the expanding species in both PCA and HCA. For *A. conyzoides*, the PCA shows the same standardized trajectory as *Tridax procumbens*, *Aspilia africana* and *Celosia leptostachya*, yet HCA assigns *Celosia leptostachya* to the expanding group and the other three to the low-density group. This indicates that HCA groups reflect density level (amplitude) as well as temporal shape. The placement of *A. conyzoides* in the low-density group therefore indicates that its density stayed low, not that its temporal pattern was unlike that of expanding associates.

Measured versus inferred mechanisms

What were measured were counts of individuals per sampling unit over time. Seed rain, seed bank, germination, clonal spread, resource availability, competition, allelopathy and light were not measured, so any mechanism discussed below is a hypothesis

and not a result. The contrast between *A. conyzoides*, an annual that reproduces mainly by abundant seed and also vegetatively (Kaur *et al.*, 2023), and the rhizomatous perennial *C. coelestinum* is biologically plausible as a contributor to the observed difference. Lateral clonal growth could add stems within quadrats over weeks, and seed-based recruitment could produce an early presence with less subsequent growth in density. Because *C. coelestinum* is rhizomatous, increases in counted stems could partly reflect clonal expansion and not new establishment, which our counts cannot separate. In Grime's (1977) framework, the early plateau of *A. conyzoides* is consistent with a ruderal strategy, and the graded rise of *C. coelestinum* could be consistent with a more competitive-ruderal position. These are interpretive labels and were not tested. Likewise, the allelopathic potential of *A. conyzoides* (Batish *et al.*, 2009) was not examined, and whether either species acts as a driver or a passenger of change (MacDougall and Turkington, 2005) cannot be resolved without removal or addition experiments.

Implications for early succession

Treating *A. conyzoides* and *C. coelestinum* as interchangeable 'early colonizers' would, in this plot, have obscured the observed difference in their net density change within the first 12 weeks of monitoring. That difference is descriptive and is not statistically supported (Section 3.2). If *C. coelestinum* continues to gain density while *A. conyzoides* remains at low density, the two could contribute differently to the early recovery trajectory, for example through different effects on later-arriving taxa. This is a hypothesis for testing, not a prediction supported by these data. It motivates distinguishing co-occurring pioneers in early-succession monitoring and fallow studies, and it suggests specific tests. These include replicated disturbance events, separate counts of ramets and genets, seedling recruitment and seed-bank sampling, and longer monitoring.

Scope of inference and limitations

The study is a single, intensively sampled disturbance event. Within that scope, it provides repeated temporal observations of seven species in each of two assemblages through six census dates. It also provides significant effects of species and of week on density within the monitored event, with the week effect weaker in Assemblage B ($p = 0.008$). It gives a comparative, descriptive contrast between the two focal species in net density change, relative density, multivariate position and CRI. It provides no statistical evidence, in this event, of a differential temporal response between species (Species × Week). Its basis for generalization is limited, because the disturbance, site and weather are confounded with the observed patterns.

The main limitations are therefore that the disturbance was not replicated, that the first census followed disturbance that counts are low, that associates were selected rather than sampled at random, and that richness was fixed at seven. The counting unit for a rhizomatous species is not separated into ramets and genets, and no environmental covariates or unburnt references were recorded. We do not regard these as reasons to dismiss the observed contrast, but they define it as hypothesis-generating. Independent replicated disturbance events, ideally with environmental covariates and a defined counting unit, are the next step to test whether the *C. coelestinum* increase and the *A. conyzoides* plateau recur.

CONCLUSION

In a single burnt-and-cleared plot, *Ageratum conyzoides* and *Conoclinium coelestinum* were both recorded from the first census at equal mean density. Their observed net density change then differed: *A. conyzoides* rose from 0.67 to 1.00 (CRI +49.3%) while *C. coelestinum* rose from 0.67 to 2.67 (CRI +298.5%), the largest increase among the 14 species analysed, and PCA and HCA placed it with the expanding species. The Species × Week interaction was not significant, so this contrast is supported by descriptive evidence and not by a formal test of differential temporal response. Life-history differences such as rhizomatous versus annual growth are plausible contributors but were not measured.

The findings show that co-occurring pioneers sharing a label can differ in early density change within one disturbance event, and they define hypotheses to be tested in replicated disturbance experiments.

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