

# Sonoran Desert Ecosystem transformation by a $C_4$ grass without the grass/fire cycle

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## ABSTRACT

**Aim** Biological invasions facilitate ecosystem transformation by altering the structure and function, diversity, dominance and disturbance regimes. A classic case is the grass–fire cycle in which grass invasion increases the frequency, scale and/or intensity of wildfires and promotes the continued invasion of invasive grasses. Despite wide acceptance of the grass–fire cycle, questions linger about the relative roles that interspecific plant competition and fire play in ecosystem transformations.

**Location** Sonoran Desert Arizona Upland of the Santa Catalina Mountains, Arizona, USA.

**Methods** We measured species cover, density and saguaro (*Carnegiea gigantea*) size structure along gradients of *Pennisetum ciliare* invasion at 10 unburned/ungrazed *P. ciliare* patches. Regression models quantified differences in diversity, cover and density with respect to *P. ciliare* cover, and residence time and a Fisher's exact test detected demographic changes in saguaro populations. Because *P. ciliare* may have initially invaded locations that were both more invulnerable and less diverse, we ran analyses with and without the plots in which initial infestations were located.

**Results** Richness and diversity decreased with *P. ciliare* cover as did cover and density of most dominant species. Richness and diversity declined with increasing time since invasion, suggesting an ongoing transformation. The proportion of old-to-young *Carnegiea gigantea* was significantly lower in plots with dominant *P. ciliare* cover.

**Main conclusions** Rich desert scrub (15–25 species per plot) was transformed into depauperate grassland (2–5 species per plot) within 20 years following *P. ciliare* invasion without changes to the fire regime. While the onset of a grass–fire cycle may drive ecosystem change in the later stages and larger scales of grass invasions of arid lands, competition by *P. ciliare* can drive small-scale transformations earlier in the invasion. Linking competition-induced transformation rates with spatially explicit models of spread may be necessary for predicting landscape-level impacts on ecosystem processes in advance of a grass–fire cycle.

## Keywords

Biological invasions, Buffelgrass, *Cenchrus ciliaris*, change point analysis, chronosequence, invasive species, *Pennisetum ciliare*, regression, succession.

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## INTRODUCTION

Invasive species have been implicated in reduced species richness (Elton, 1958; Sanders *et al.*, 2003; Jackson, 2005; Gaertner *et al.*, 2009; Hejda *et al.*, 2009), changes in ecosystem

structure (Forseth & Innis, 2004) and function (Vitousek & Walker, 1989), and altered disturbance regimes, notably fire (D'Antonio & Vitousek, 1992). Often, these impacts interact to promote the continued invasion and transformation of ecosystems (D'Antonio & Vitousek, 1992). The classic example

is the grass–fire cycle, wherein fire-prone grasses invade ecosystems with infrequent or rare fire return intervals, increase the frequency and/or intensity of wildfires and thus reduce the abundance of less fire-tolerant natives while introduced grasses recover and prosper (D’Antonio & Vitousek, 1992; Brooks *et al.*, 2004). Inception of a grass/fire cycle (GFC) is one of many ways in which an ecosystem can become ‘transformed’ as a result of invasion. Richardson *et al.* (2000) define ‘transformers’ as those whose invasion alters ‘the character, condition, form, or nature of ecosystems over substantial areas’.

The evidence for a grass–fire cycle is compelling for many exotic grass invasions, including both C<sub>3</sub> grasses (Beatley, 1966; Whisenant, 1990; Brooks, 1999) and C<sub>4</sub> grasses (D’Antonio & Vitousek, 1992; D’Antonio *et al.*, 2001; Burquez-Montijo *et al.*, 2002, Rossiter *et al.*, 2003; Hoffman *et al.*, 2004; Daehler & Goergen, 2005) and is often invoked in motivating political will and pre-emptive action to avert ecosystem transformation. While the potential for GFCs has captured the attention of managers and ecologists alike, we feel that additional mechanisms of transformation operating at different spatial and temporal scales may be overlooked as a result of the focus on fire.

Grasses have repeatedly been shown to interfere with woody plant recruitment (Litton *et al.*, 2006; Hoffman & Haridasan, 2008), woody plant growth (Clary *et al.*, 2005), carbon dynamics (Litton *et al.*, 2006, 2008) and ecosystem structure (Litton *et al.*, 2006; Lambrinos, 2000). Perennial C<sub>4</sub> African bunchgrasses in particular have been shown to negatively influence leaf mass in dominant woody plants (Cordell & Sandquist, 2008), alter resource acquisition rates and timing (Williams & Baruch, 2000; Cordell & Sandquist, 2008), lower species richness (Jackson, 2005; Franklin & Molina-Freaner, 2010) and inhibit recruitment of both woody plants (D’Antonio *et al.*, 1998; Litton *et al.*, 2006) and columnar cacti (Morales-Moreno & Molina-Freaner, 2008). Studies have confirmed that competition by invasive grasses may play an important role in ecosystem transformation although the role of fire in transformation is typically complimentary and separation of the two is not clear (e.g. Litton *et al.*, 2006).

In the Arizona Upland vegetation zone of the Sonoran Desert, ongoing invasion by the African C<sub>4</sub> perennial bunchgrass, *Pennisetum ciliare*, is expected to initiate a GFC in an ecosystem that rarely burns (Mclaughlin & Bowers, 1982; Thomas, 1991). Previous Sonoran Desert wildfires have been devastating to native vegetation, notably *Carnegiea gigantea* and *Parkinsonia microphylla* (Mclaughlin & Bowers, 1982; Schmid & Rogers, 1988; Narog & Wilson, 2005). *P. ciliare* was introduced to the Sonoran Desert in 1938 for erosion control or cattle forage as part of a world-wide search for a ‘wonder grass’ (Cox *et al.*, 1988). *P. ciliare* is widely known as a fire-promoting grass and has been implicated in a grass–fire cycle in Sonora, Mexico (Burquez-Montijo *et al.*, 2002), Hawaii (Daehler & Goergen, 2005) and Australia (Clarke *et al.*, 2005; Fairfax & Fensham, 2000). Its potential for transforming the

ecosystem and introducing a grass–fire cycle in the Sonoran Desert has served as a rallying point for listing *P. ciliare* as a noxious weed of Arizona (see Arizona statute ARIZ R3-4-244), the development of a Buffelgrass Strategic Plan (Rogstad, 2008), establishment of a non-profit Southern Arizona Buffelgrass Coordination Center, development of a state-of-the-art data management system and decision support model, and accelerated control efforts by public agencies and volunteers (<http://www.buffelgrass.org>).

However, even in the absence of fire, Arizona Upland ecosystems appear to experience dramatic declines in species richness and structural heterogeneity, raising questions about the relative value of keeping fire out of post-invaded ecosystems. More generally, the issue raised is: To what extent will fire suppression over small and large spatial scales benefit native Arizona Upland conservation in the face of ongoing *P. ciliare* invasion?

## OBJECTIVES

We sought to document the differences between undisturbed native Sonoran Desert and *P. ciliare*-invaded ecosystems, notably differences in perennial plant richness, diversity and abundance of dominant species, as well as estimate potential rates in which those differences may have arisen following invasion. We posit that, in the absence of fire, native plant abundance (both dominant and subdominant) is declining and vegetation structure is changing with increasing *P. ciliare* abundance and time since invasion. We used a space-for-time substitution in which we measured and compared perennial plant communities in plots of increasing *P. ciliare* cover and time since invasion. Since climate variability may have influenced the interactions of *P. ciliare* and natives over time, we present our results in the context of potential climate interactions.

## METHODS

### Study areas

This study was conducted at the lowest southern slopes of the Santa Catalina Mountains in southern Arizona, USA, in habitat typical of the Arizona Upland (Turner & Brown, 1994) (Fig. 1). The sparse (25–35%) canopy cover is dominated by the small tree, palo verde (*Parkinsonia microphylla*), the short-lived shrub (*Encelia farinosa*), the iconic saguaro cactus (*Carnegiea gigantea*), and numerous other trees, shrubs, cacti, grasses and forbs (Turner & Brown, 1994). Based on a 41-year record (1941–1982) of the nearest COOP Station (#027355), mean annual precipitation (32.3 cm) is bimodally distributed, with slightly more precipitation falling regularly during the summer, when *P. ciliare* is most active photosynthetically (WRCC 2011).

In winter 2008–2009, we identified a total of 10 *P. ciliare* patches of differing size at three sites: Campbell (CAMP), Melpomene (MELP) and Agua Caliente (AGUA) within an

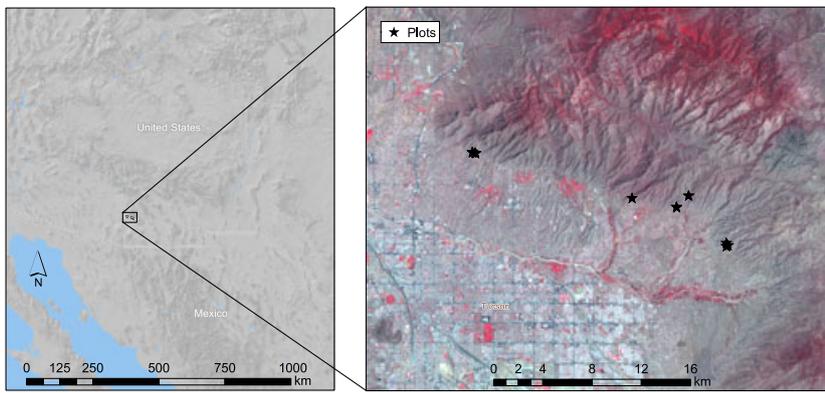


Figure 1 Map of study sites showing its proximity to Tucson, AZ.

elevation range of 883–1097 m. Patches ranged from 29 to 126, 098 m<sup>2</sup> (mean patch size was 20,098 m<sup>2</sup>). At each patch, we constructed transects of contiguous 11 × 11 m plots originating at the patch centre and ending at least 20 m outside the patch (Fig. 2). Transects were randomly oriented but confined to similar slope, aspect and geomorphology. The locations of each site were cross-referenced against the Coronado National Forest fire history database. Fires had been reported near two transects (AGUA-2 in 1994 and MELP-3 in 2003), but site-level surveys did not reveal evidence of fire.

All sites were surveyed for evidence of fire in the form of subterranean charcoal skins up to 20 cm in depth and as fire scars on saguaro cacti. As we did not find signs of fire, no plots were thrown out. A photograph of one of the smallest patches (AGUA-2) is given in Fig. 3.

### Cover and density measures

Species cover was estimated at each plot using the point-intercept method on a regular grid at 1-m intervals, making a total of 121 intercepts per plot (Bonham, 1989). Where more than one canopy level was intersect, each species was recorded. Density was calculated by tallying the number of each individual within the plot and dividing by the area. Heights of each saguaro was recorded using a tape (<200 cm) or estimated visually (≥200 cm).

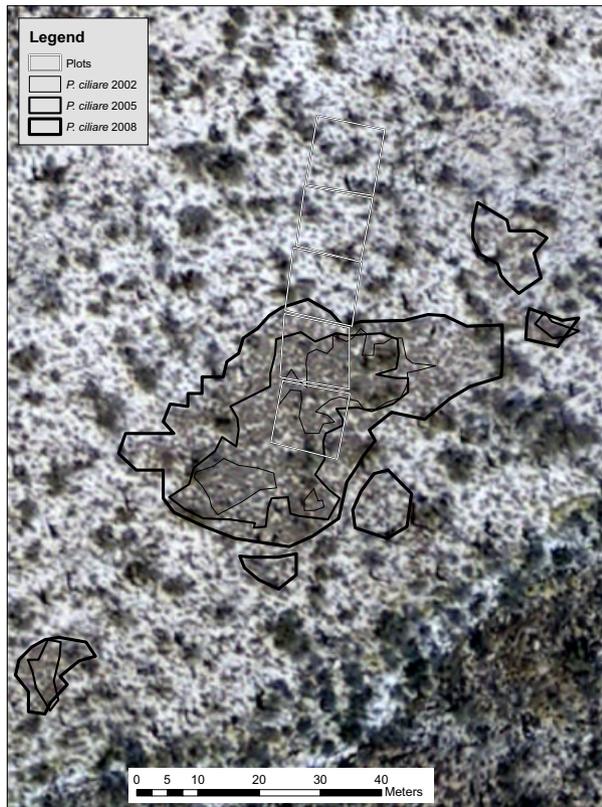


Figure 2 Example of AGUA-2 site with plot boundaries (white rectangles) and historic patch boundaries from 2002, 2005 and 2008. Image background is 0.3 m imagery from the Pima Association of Governments, acquired in 2008.



Figure 3 This photograph of AGUA-2 site taken in 2008 shows a relatively small patch (211 m<sup>2</sup>) on a native-dominated hillslope north-east of Tucson, AZ. The *P. ciliare* patch (a) is characterized by few trees and shrubs amid a relatively homogeneous grassy matrix. A secondary outbreak (b) has developed downslope from the original infestation. The dominant tree is *Parkinsonia microphylla* (c), with a mean height of close to 5 m on this slope. The saguaro cactus (*Carnegiea gigantea*) is the dominant columnar cactus in this ecosystem (d).

### Time since invasion

A conservative estimate of invasion date was made for each plot using historical aerial imagery available for every plot. The initial invasion date was assigned to each plot based on the earliest date when *P. ciliare* was positively identified in aerial imagery. Aerial photography was acquired from multiple sources, including a private vendor (Cooper Aerial, Inc.) and Pima Association of Governments (PAG). Aerial photographs obtained from the private vendor were registered to a 2005 USGS Digital Orthophoto Quarter Quad using a rubbersheet model with 20–30 ground control points used for each photograph, but accuracy was only necessary in the immediate vicinity of each plot. Ridgelines and valleys were critical for accurate registration because of the various oblique angles that aerial photography was collected at, although rock outcrops, soil disturbances, and man-made objects were also used. PAG imagery was rectified prior to our receiving it. A map of the reconstructed spread over a *c.* 400 ha area covering two transects and 14 of our plots is shown in Fig. 4.

### Terminology

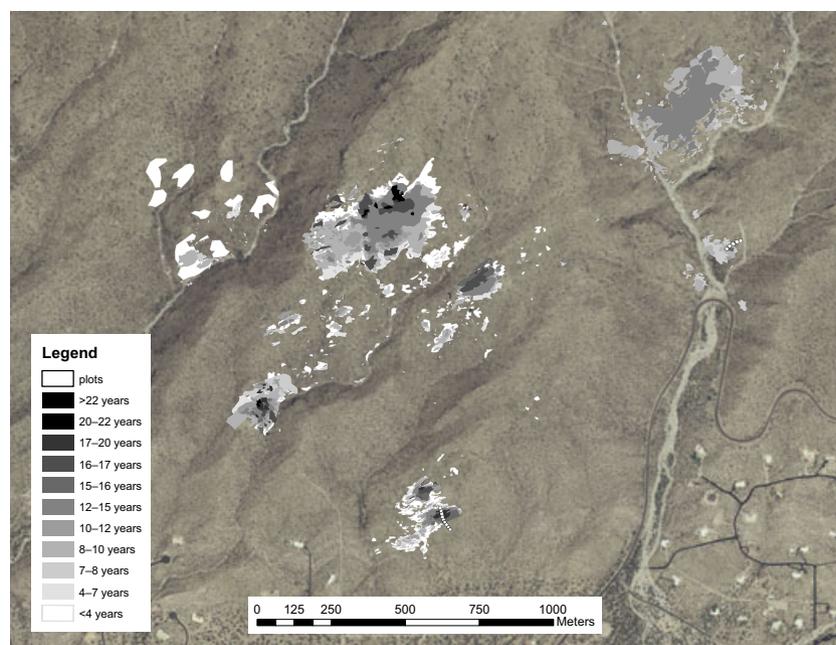
Hereafter, we use the terms ‘uninvaded’ and ‘invaded’, to refer to plots with  $<5\%$  *P. ciliare* and  $\geq 5\%$  *P. ciliare*, respectively. In addition, ‘time since invasion’ refers to the number of years before the 2009 field measurements in which *P. ciliare* cover was positively identified on a plot via aerial imagery interpretation.

### Statistical analysis

The following metrics were calculated for each plot: cover and density by species, cover and density by functional type as

defined by the USDA Plants Profile for each species (trees, shrubs, succulents, forbs, and grasses (excluding *P. ciliare*)), species richness (excluding *P. ciliare*) and Shannon’s diversity (derived from density excluding *P. ciliare*). Because densities were not normally distributed, a square-root transformation was applied to density values (Sokal & Rohlf, 1995). To describe the influence of *P. ciliare* abundance, each metric was regressed against percent *P. ciliare* cover. To identify the critical thresholds of *P. ciliare* cover above which diversity and richness declined more rapidly, we performed change point analysis on diversity and richness trends with respect to *P. ciliare* cover. Change point analysis identifies an index in an ordered series before and after which means or variances of the series are different (Perreault *et al.*, 2000). We ordered the plot data by increasing *P. ciliare* cover and used the ‘bcp’ package (version 2.2) in R to perform the analysis (Erdman & Emerson, 2010). Because multiple plots had the same *P. ciliare* cover, we used a Monte Carlo approach to randomize the order of plots with the same *P. ciliare* cover over 100 runs for each metric (diversity and richness). To describe the influence of time since invasion, multiple regressions based on only the plots with *P. ciliare* cover greater than the change point were calculated using *P. ciliare* cover and time since invasion as explanatory variables. Although transects were selected to allow investigations of differences along a gradient from uninvaded to long-infested, we could not completely rule out the possibility that changes in diversity and individual species abundances could not be explained by existing (unmeasured) conditions that simultaneously led to increased invasibility and to differences along this gradient. Therefore, we performed each analysis with and without the plots in which *P. ciliare* had been established the longest. For models in which time since invasion was significant, we developed a third model based only on the initial invasion plots. We identified the plots on which *P. ciliare*

**Figure 4** Map of historical buffelgrass spread at Soldier Canyon (a region of the ‘MELP’ site) near Tucson, AZ. Locations of two transects are also shown. Note that image availability differed for each date, resulting in slightly differing temporal precision across the image. The ages represent the earliest documentation that buffelgrass was detected via aerial image interpretation at a given location.



invaded in the earliest photo as the 'initial invasion plots'. Plots infested after the date of initial invasion were identified as 'secondary invasion plots'. To describe the influence on saguaro size structure, a Fisher's exact test was used to compare the differences in the proportion of small-to-large (<200 cm vs.  $\geq 200$  cm) saguaros in relation to *P. ciliare* cover.

## RESULTS

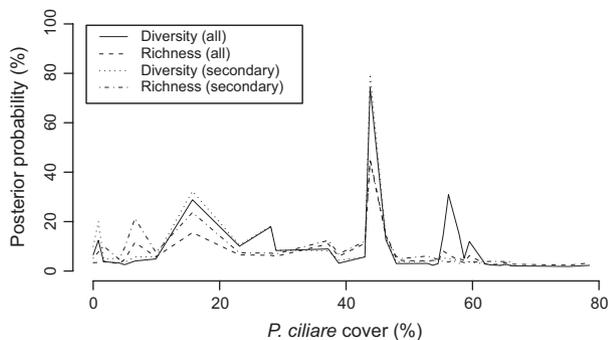
Of the 49 plots in this study, 12 were identified as initial invasion plots, leaving 37 as secondary invasion plots. Ten initial and 14 secondary invasion plots had *P. ciliare* cover greater than the change point (described below) and defined the plots used in multiple regressions of *P. ciliare* cover and time since invasion. A total of 118 saguaros were measured in the plots, of which 15 and 103 were located in initial and secondary invasion plots, respectively.

### Change point analysis

The strongest change point occurred at 43.8% *P. ciliare* cover for richness and diversity based on both the full set of plots and the secondary invasion plots (Fig. 5). Posterior probabilities suggested that a strong change in means or variances of richness and diversity occurred above and below 43.8% plots with *P. ciliare* cover. Hereafter, we use the 43.8% *P. ciliare* change point as a threshold for including plots in multiple regressions involving *P. ciliare* and time since invasion.

### Species richness and diversity

Species richness was lower by 0.165 ( $\pm 0.0210$  SE) and 0.146 ( $\pm 0.0253$ ) species per 1% increase in *P. ciliare* cover based on all plots ( $n = 49$ ,  $P < 0.0001$  for the *P. ciliare* cover coefficient, Adj.  $R^2 = 0.560$ ) and secondary invasion plots ( $n = 37$ ,  $P < 0.0001$ , Adj.  $R^2 = 0.473$ ) (Table 1, Fig. 6). Among plots with at least 43.8% *P. ciliare* cover (above the change point), species richness was lower by 0.301 ( $\pm 0.0643$ ) species per year



**Figure 5** Change point plot showing probability that means and/or variances of diversity and richness are different above and below certain *P. ciliare* thresholds. Two lines each for diversity and richness are based on looking for change points among all plots (all) or only among secondary invasion plots (secondary).

after accounting for variations in *P. ciliare* cover in all plots ( $P = 0.0001$ , Adj.  $R^2 = 0.495$ ), but the relationship was not significant when looking only at secondary invasion plots ( $P = 0.085$ , Adj.  $R^2 = 0.112$ ). Diversity was lower by 0.0223 ( $\pm 0.00179$ ) and 0.0200 ( $\pm 0.00206$ ) per 1% in *P. ciliare* cover based on all plots ( $P < 0.0001$ , Adj.  $R^2 = 0.763$ ) and secondary invasion plots only ( $P < 0.0001$ , Adj.  $R^2 = 0.762$ ). Among plots with at least 43.8% *P. ciliare* cover, diversity was lower by 0.0457 ( $\pm 0.00607$ ) per year ( $n = 31$ ,  $P = 0.0006$ , Adj.  $R^2 = 0.681$ ) after accounting for variations in *P. ciliare* cover, but was not significantly lower with respect to just the secondary invasion plots with  $\geq 43.8\%$  *P. ciliare* cover ( $P = 0.251$ ).

### Effects on species

In uninvaded plots, the ten most abundant species by cover ranged from 1.65% to 16.1% mean cover (Table 1). Of those ten species, seven were significantly negatively correlated with *P. ciliare* cover, although this dropped to three species when comparing just among secondary invasion plots: *Encelia farinosa*, *Janusia gracilis*, *Calliandra eriophylla* and *Jacquemontia pringlei*. The ten most abundant species by density ranged from 0.029 to 0.461 plants/m<sup>2</sup> (Table 2). Of those, seven were significantly negatively correlated with *P. ciliare* cover in all plots (including the top six), and six were significant when comparing just among secondary invasion plots: *E. farinosa*, *Evolvulus arizonica*, *Mammillaria grahamii*, *Abutilon incanum*, *C. eriophylla* and *J. gracilis*.

Two of the top ten species by cover were significantly (negatively) correlated with years since invasion in plots with  $\geq 43.8\%$  *P. ciliare* (*Encelia farinosa* and *Parkinsonia microphylla*) and, of those, only *P. microphylla* cover was significantly lower in all plots and in secondary invasion plots (Table 3). Using only the 12 initially infested plots, *P. microphylla* decreased by 0.618% per year after accounting for *P. ciliare* cover ( $P = 0.0383$  for the coefficient of time since invasion, adjusted  $R^2 = 0.402$  for the model). The only significant relationship between density and years since invasion was with *C. eriophylla*, which had a positive correlation with time on secondary invasion plots but no significant correlation among all plots (Table 4).

*C. gigantea* cover and density were not significantly correlated with either *P. ciliare* cover or time since invasion, although fewer small ( $\leq 2$  m) *C. gigantea* were found in plots with  $\geq 43.8\%$  *P. ciliare* than expected given densities outside infested areas when examining saguaros in all plots ( $P = 0.008$ ,  $n = 118$  saguaros in a right-tailed Fisher's exact test) or secondary invasion plots ( $P = 0.0108$ ,  $n = 103$ ), and the size structure indicates a general lack of small saguaros in increasing *P. ciliare* cover (Fig. 7).

### Effects on functional types

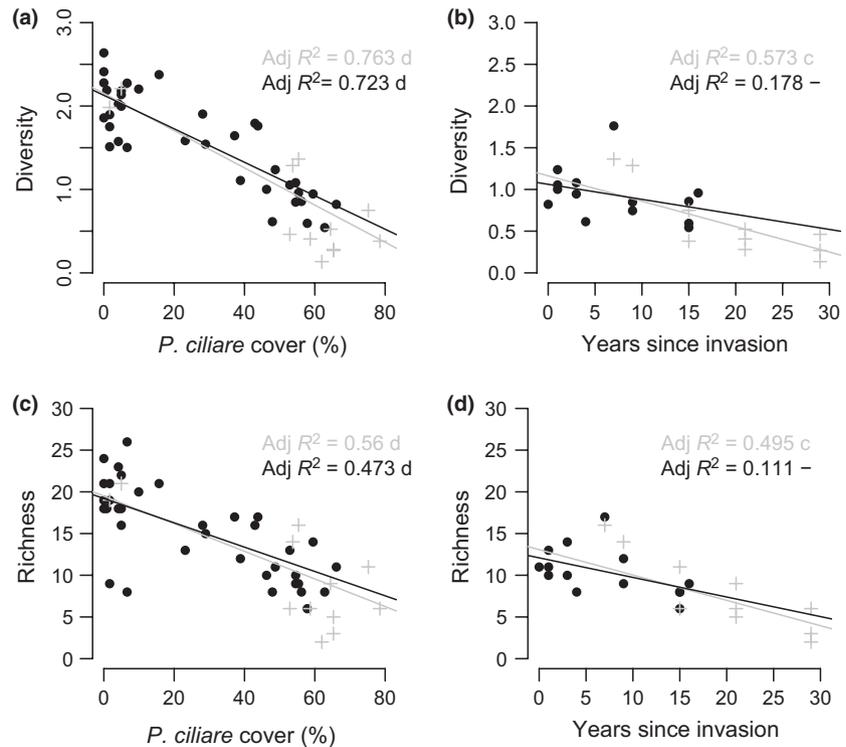
Cover of shrubs, forbs, grasses (sans *P. ciliare*) and succulents were negatively correlated with *P. ciliare* cover based on all

**Table 1** Regression coefficients of species cover with respect to increasing *P. ciliare* cover including all plots ( $n = 49$ ) and only secondary invasion plots ( $n = 37$ ) for 15 most abundant species in uninvaded (*P. ciliare* cover < 5%) plots.

Species	Uninvaded cover Mean % (SE)	Regression results (all plots)		Regression results (secondary invasion plots)	
		Slope	Adj. $R^2$	Slope	Adj. $R^2$
<i>Encelia farinosa</i>	16.14 (1.46)	-0.232 <sup>d</sup>	0.705	-0.2295 <sup>d</sup>	0.635
<i>Parkinsonia microphylla</i>	12.56 (2.24)	-0.098 <sup>a</sup>	0.060		
<i>Prosopis glandulosa</i>	3.80 (2.10)				
<i>Janusia gracilis</i>	3.20 (1.08)	-0.049 <sup>b</sup>	0.172	-0.049 <sup>a</sup>	0.123
<i>Jatropha cardiophylla</i>	2.98 (1.00)	-0.033 <sup>a</sup>	0.087		
<i>Lycium berlandieri</i>	2.26 (0.68)	-0.024 <sup>a</sup>	0.093		
<i>Fouquieria splendens</i>	1.93 (0.43)				
<i>Calliandra eriophylla</i>	1.76 (0.52)	-0.027 <sup>c</sup>	0.214	-0.026 <sup>a</sup>	0.159
<i>Eysenhardtia orthocarpa</i>	1.76 (1.08)				
<i>Jacquemontia pringlei</i>	1.65 (0.85)	-0.034 <sup>a</sup>	0.114	-0.040 <sup>a</sup>	0.100
<i>Abutilon incanum</i>	1.60 (0.60)	-0.023 <sup>b</sup>	0.151	0.024 <sup>a</sup>	0.116
<i>Cylindropuntia versicolor</i>	1.38 (0.55)				
<i>Evolvulus arizonica</i>	1.32 (0.56)	-0.019 <sup>b</sup>	0.138	-0.024 <sup>a</sup>	0.136
<i>Opuntia engelmannii</i>	1.16 (0.95)				
<i>Trixis californica</i>	0.88 (0.35)	-0.012 <sup>a</sup>	0.110		
All succulents	5.5 (1.3)	-5.45 <sup>b</sup>	0.146	-5.28 <sup>a</sup>	0.092
All grasses	2.1 (0.43)	-3.56 <sup>d</sup>	0.309	-3.84 <sup>c</sup>	0.255
All forbs	3.1 (1.0)	-1.29 <sup>c</sup>	0.210	-1.41 <sup>c</sup>	0.170
All shrubs	31.7 (1.7)	-40.38 <sup>d</sup>	0.643	-34.4 <sup>d</sup>	0.655
All trees	16.7 (2.8)	-14.15 <sup>b</sup>	0.122		0.033

Similar metrics are given for plant functional type cover (bottom). Significance is denoted by superscripts <sup>a</sup>( $P < 0.05$ ), <sup>b</sup>( $P < 0.01$ ), <sup>c</sup>( $P < 0.001$ ), or <sup>d</sup>( $P < 0.0001$ ). Insignificant relationships are left blank.

**Figure 6** Scatter plots of Shannon's diversity and species richness vs. *P. ciliare* cover and time since invasion. Sampling plots associated with initial infestations are denoted by grey crosses (+). All models that exclude initial invasion plots are denoted by grey test statistics and grey fit lines. Statistics in a) and c) are based on single regression of richness/diversity vs. *P. ciliare* cover. Significance of the coefficients is denoted by 'd' ( $p < 0.0001$ ), 'c' ( $p < 0.001$ ), 'b' ( $p < 0.01$ ), 'a' ( $p < 0.05$ ) and '-' ( $p \geq 0.05$ ). Statistics b) and e) are based on the multiple regression of richness/diversity vs. *P. ciliare* cover and years since invasion using plots with > 43.6% *P. ciliare* cover. The  $p$ -values of the coefficient for years since invasion are denoted by a letter.



Species	Uninvaded Mean density (SE)	Regression results (all plots)		Regression results (secondary invasion plots)	
		Slope	Adj. R <sup>2</sup>	Slope	Adj. R <sup>2</sup>
<i>Encelia farinosa</i>	0.461 (0.077)	-0.625 <sup>d</sup>	0.419	-0.645 <sup>c</sup>	0.335
<i>Mammillaria grahamii</i>	0.371 (0.051)	-0.513 <sup>d</sup>	0.458	-0.492 <sup>d</sup>	0.337
<i>Evolvulus arizonica</i>	0.164 (0.062)	-0.246 <sup>c</sup>	0.136	-0.293 <sup>a</sup>	0.127
<i>Abutilon incanum</i>	0.131 (0.032)	-0.188 <sup>d</sup>	0.231	-0.177 <sup>b</sup>	0.166
<i>Calliandra eriophylla</i>	0.109 (0.030)	-0.144 <sup>b</sup>	0.177	-0.137 <sup>a</sup>	0.108
<i>Lycium berlandieri</i>	0.072 (0.038)				
<i>Janusia gracilis</i>	0.070 (0.019)	-0.092 <sup>c</sup>	0.166	-0.898 <sup>a</sup>	0.127
<i>Jacquemontia pringlei</i>	0.052 (0.027)	-0.099 <sup>a</sup>	0.108		
<i>Jatropha cardiophylla</i>	0.030 (0.015)				
<i>Muhlenbergia porter</i>	0.029 (0.004)				
<i>Parkinsonia microphylla</i>	0.028 (0.009)	-0.024 <sup>b</sup>	0.122		
<i>Trixis californica</i>	0.023 (0.008)	-0.027 <sup>a</sup>	0.010		
<i>Carnegiea gigantea</i>	0.022 (0.008)				
<i>Heteropogon contortus</i>	0.022 (0.008)	-0.057 <sup>a</sup>	0.096		
All succulents	0.45 (0.060)	-68.7 <sup>d</sup>	0.419	-62.6 <sup>c</sup>	0.306
All grasses	0.11 (0.038)	-0.035 <sup>c</sup>	0.309	-0.038 <sup>c</sup>	0.255
All forbs	0.32 (0.082)	-81.4 <sup>d</sup>	0.268	-89.3 <sup>b</sup>	0.229
All shrubs	0.76 (0.098)	-102.2 <sup>d</sup>	0.482	-103.7 <sup>c</sup>	0.387
All trees	0.028 (0.0040)	-3.19 <sup>b</sup>	0.189	-2.86 <sup>a</sup>	0.119

Similar metrics are given for plant functional type cover (bottom). Significance is denoted by superscripts <sup>a</sup>( $P < 0.05$ ), <sup>b</sup>( $P < 0.01$ ), <sup>c</sup>( $P < 0.001$ ), or <sup>d</sup>( $P < 0.0001$ ). Insignificant relationships are left blank.

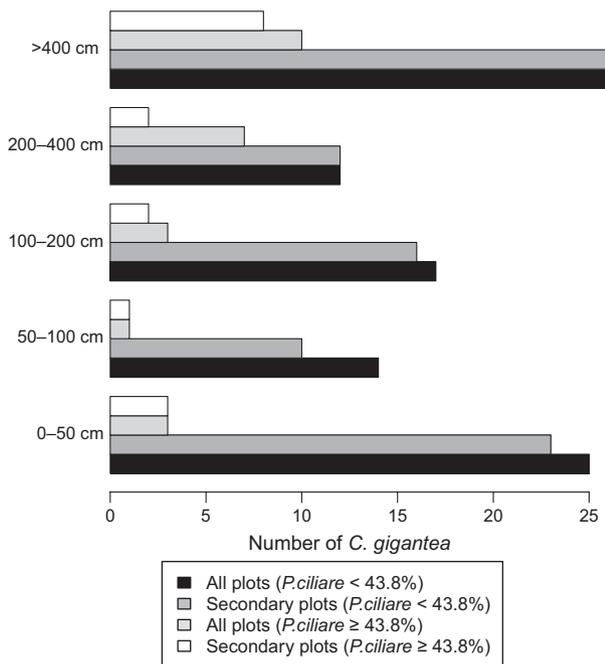


Figure 7 Histogram of *C. gigantea* count by size class in two levels of *Pennisetum ciliare* in all plots and in secondary invasion plots.

plots and secondary invasion plots with one exception: tree cover was not significantly correlated with *P. cilare* cover in secondary invasion plots (Table 1, Fig. 8). Conversely, only

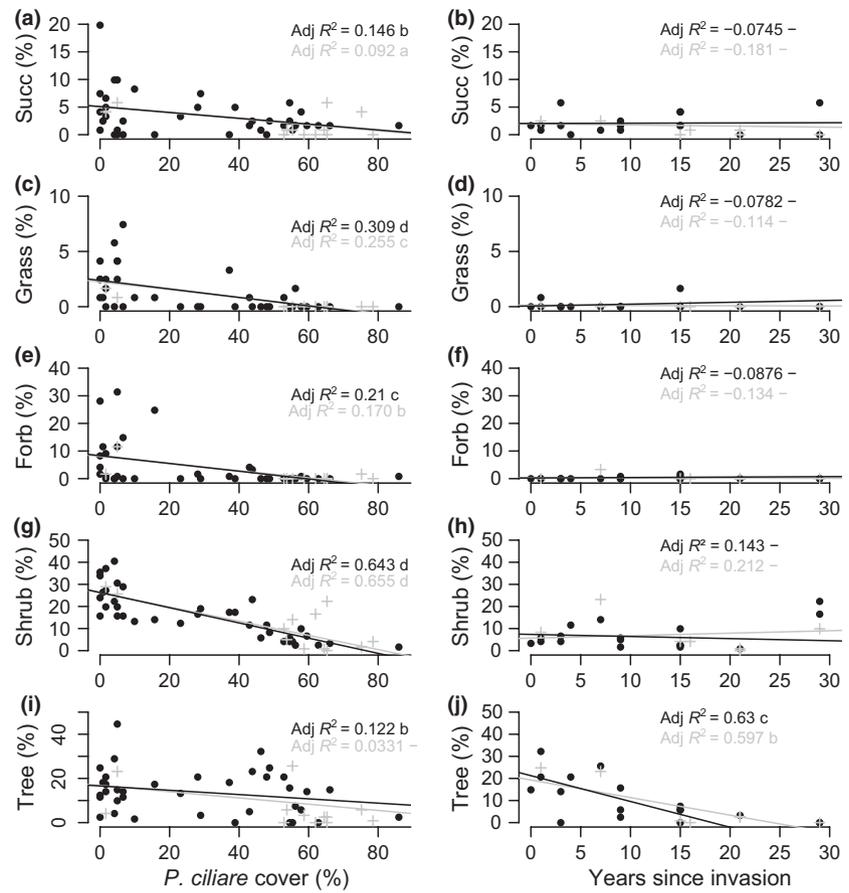
Table 2 Regression coefficients of species density with respect to increasing *P. ciliare* cover including all plots ( $n = 49$ ) and only secondary invasion plots ( $n = 37$ ) for 15 most abundant species in uninvaded (*P. ciliare* cover < 5%) plots.

trees were significantly negatively correlated with years since invasion (based on all plots and secondary invasion plots). In plots with  $\geq 43.8\%$  *P. ciliare* cover, tree cover was approximately 9.8% and 6.7% lower per decade after invasion based on all plots and secondary invasion plots, respectively.

## DISCUSSION

We document ecosystem transformation of a diverse and undisturbed desert scrub ecosystem dominated by CAM succulents and  $C_3$  perennials into a depauperate  $C_4$  grass-dominated ecosystem in response to increasing abundance and residence time of the well-known fire-promoting grass, *P. ciliare*, but without fire. Every major functional type present in uninvaded plots was significantly reduced with either increasing *P. ciliare* cover or time since initial invasion. Grass cover, which was less abundant than trees, shrubs, succulents and forbs in uninvaded plots, was easily the most dominant plant on the interior of *P. ciliare* patches. The patterns of decline in three dominant Arizona Upland species (*Carnegiea gigantea*, *Parkinsonia microphylla* and *Encelia farinosa*) highlight a number of potential mechanisms by which *P. ciliare* transforms this ecosystem and may provide the basis of a successional model that describes the transformation of Arizona Upland desert scrub by *P. ciliare*.

The youngest cohort of *C. gigantea* (individuals < 200 cm in height) was markedly lower in invaded plots vs. uninvaded and partially invaded plots, portending a long-term decline in



**Figure 8** Left column (a, c, e, g, i): Plant functional type (PFT) cover with respect to *P. ciliare* cover. Adjusted  $R^2$  values for models PFT vs. *P. ciliare* cover are based on all plots (black) or secondary invasion plots only. Model significance is denoted by ‘a’ ( $p < 0.05$ ), ‘b’ ( $p < 0.01$ ), ‘c’ ( $p < 0.001$ ) and ‘d’ ( $p < 0.0001$ ). Right column (b, d, f, h, j): PFT cover with respect to time since invasion. Model statistics are based on multiple regressions of PFT cover by *P. ciliare* cover and time since invasion using only plots above the 43.8% change point. Black and grey distinguish models that used all plots with  $\geq 43.8\%$  and only secondary invasion plots with *P. ciliare* cover  $\geq 43.8\%$ .

**Table 3** Regression coefficients of species cover with respect to increasing *P. ciliare* cover and invasion time including all plots  $\geq 43.8\%$  ( $n = 24$ ) and only secondary invasion plots  $\geq 43.8\%$  ( $n = 14$ ) for five most abundant species in uninvaded (*P. ciliare* cover < 5%) plots.

Species	All plots			Secondary invasion plots		
	Adj. $R^2$	<i>P. ciliare</i>	Years	Adj. $R^2$	<i>P. ciliare</i>	Years
<i>Encelia farinosa</i>	0.445	-0.153 <sup>b</sup>	-0.011 <sup>a</sup>	0.296	-0.197 <sup>a</sup>	
<i>Parkinsonia microphylla</i>	0.637	-0.394 <sup>b</sup>	-0.007 <sup>c</sup>	0.628	-0.447 <sup>a</sup>	-0.111 <sup>b</sup>
<i>Prosopis glandulosa</i>						
<i>Janusia gracilis</i>						
<i>Jatropha cardiophylla</i>						
All succulents	-0.075			-0.181		
All grasses	-0.078			-0.114		
All forbs	-0.088			-0.134		
All shrubs	0.143	-0.292 <sup>a</sup>		0.212	-0.309 <sup>a</sup>	
All trees	0.630	-0.391 <sup>b</sup>	-0.007 <sup>c</sup>	0.597	-0.468 <sup>a</sup>	-0.010 <sup>b</sup>

Similar metrics are given for plant functional types (bottom). Significance is denoted by superscripts <sup>a</sup>( $P < 0.05$ ), <sup>b</sup>( $P < 0.01$ ), or <sup>c</sup>( $P < 0.001$ ). Insignificant relationships are left blank.

*C. gigantea* as a result of a lack of recruitment. Based on age-height charts developed for *C. gigantea* populations in the nearby Tumamoc Hill [Correction added on 23 November 2011, after first online publication: name of location rectified], which have similar topography and climate, individuals between 50 and 200 cm tall are likely between 15 and 40 years old (Pierson & Turner, 1998). Noting that the majority of plots appear to have been largely free of *P. ciliare* 15–40 years ago, we

surmise that the reduced proportion of young-to-old saguaros in *P. ciliare*-dominated plots is attributed to (1) limited recruitment ahead of invasion, (2) recruitment inhibition following invasion or (3) elevated juvenile mortality. In the first case, the apparent lack of young saguaros could account for a gap that made the site more invulnerable. Indeed, we did not find evidence to disprove this hypothesis nor did we collect data to support or invalidate the second potential cause: recruitment

Species	All plots			Secondary invasion plots		
	Adj. $R^2$	<i>P. ciliare</i>	Years	Adj. $R^2$	<i>P. ciliare</i>	Years
<i>Encelia farinosa</i>	0.284	-0.267				
<i>Mammillaria grahamii</i>						
<i>Evolvulus arizonica</i>						
<i>Abutilon incanum</i>						
<i>Calliandra eriophylla</i>				0.275		0.0021 <sup>a</sup>
All succulents	0.297		-0.598 <sup>a</sup>			
All grasses						
All forbs						
All shrubs						
All trees	0.177		-0.094 <sup>a</sup>			

Similar metrics are given for plant functional types (bottom). Significance is denoted by the superscript <sup>a</sup>( $P < 0.05$ ). Insignificant relationships are left blank.

inhibition. However, *P. ciliare* has been documented to limit the first-year survival of seedlings of the columnar cactus, *Pachycereus pecten-aboriginum*, further south in the Sonoran Desert (Morales-Moreno & Molina-Freaner, 2008) and in greenhouse experiments, *P. ciliare* exhibits allelopathy on a number of annual and perennial forb and grass seeds (Hussain et al., 2011), demonstrating another mechanism for potentially limiting *C. gigantea* recruitment. We found evidence to support the third hypothesis at several of our study sites in the form of increased rodent activity. The white-throated woodrat (*Neotoma albigula*) utilizes succulent stems as a source of water, preferring *Opuntia* and *Cylindropuntia* species, but utilizing *C. gigantea* as well, particularly in times of drought (Steenbergh & Lowe, 1977). We found large numbers of *C. gigantea* of all sizes with girdling damage characteristic of *N. albigula*. Noting also that *Opuntia* and succulent densities in general were lower in *P. ciliare* patch interiors, *N. albigula* may have switched diets to *C. gigantea*, one of the few succulents available in *P. ciliare* patches. Increased grass cover may afford increased protection from predators as well, allowing rodent populations and water resource pressure to rise. *C. gigantea* is a keystone species and a cultural icon of the Sonoran Desert, and its protection is mandated by the Native Plant Protection Act. Understanding its response to *P. ciliare* invasion is of concern to most landowners in the Sonoran Desert. Therefore, we encourage further research into the potentially complex interactions between *P. ciliare* and *C. gigantea*.

Neither *P. microphylla* cover nor density was significantly lower with increasing *P. ciliare* cover in secondary invasion plots, but in plots with  $\geq 43.8\%$  *P. ciliare* cover, the models describing *P. microphylla* cover vs. *P. ciliare* cover and time since invasion were significant, with time since invasion explaining more of the variance than *P. ciliare* cover. Once again, the pattern can be described by *P. ciliare* as a cause or by pre-existing conditions that made the site both invasible and explain the low *P. microphylla* cover—namely, that a lack of *P. microphylla* at the site may have pre-conditioned the site for invasion. We suggest that the second hypothesis is unlikely;

when the originally infested plots were removed from analysis, the model was actually stronger than the model that included all plots. Furthermore, the model based solely on the initial invasion plots demonstrated a significant negative correlation with time. If a pre-existing condition were responsible for both *P. ciliare* invasion and lower *P. microphylla* cover, then this result suggests that more recent initial infestations are occurring in more diverse locations than initial infestations from decades ago. We also found dead *P. microphylla* skeletons and noted abundant self-pruning of *P. microphylla* individuals on the interiors of patches although these observations were not quantified. If *P. ciliare* is indeed the cause of this pattern, as we suggest, it apparently takes a number of years for *P. ciliare*–*P. microphylla* interactions to result in either self-pruning or mortality of *P. microphylla*, both of which are common responses to drought that result in reduced cover (Bowers & Turner, 2001). In 2002–2003, droughts in the Sonoran Desert resulted in widespread mortality of *P. microphylla* and other long-lived trees and shrubs (Bowers, 2005). If *P. microphylla* individuals had to cope with a dense network of shallowly rooted *P. ciliare* in addition to drought, we speculate that *P. microphylla* mortality would have been greater in *P. ciliare* patches during this time than the background mortality that uninvaded Arizona Upland landscapes experienced. While the mechanisms are not explored here, *P. microphylla* is one of the most abundant long-lived species in this ecosystem, and understanding its interactions with invasive *P. ciliare* in the absence of fire is important for managing this ecosystem in the face of ongoing invasion.

The decline of the most ubiquitous shrub in our uninvaded plots, *E. farinosa*, appears more immediately tied to an increase in *P. ciliare* cover. *E. farinosa* is a short-lived shrub with shallow, ephemeral roots and a mean life span of 16 years (Bowers, 2005) whose growth is primarily limited by water (Ehleringer, 1984). We found very little *E. farinosa* in plots with  $>50\%$  *P. ciliare* cover and, among the nine plots with 60% *P. ciliare* cover or more (three of which were secondary invasion plots invaded 0, 9, and 15 years), only two had a

**Table 4** Regression coefficients of species density with respect to increasing *P. ciliare* cover and invasion time including all plots  $\geq 43.8\%$  ( $n = 24$ ) and only secondary invasion plots  $\geq 43.8\%$  ( $n = 14$ ) for five most abundant species in uninvaded (*P. ciliare* cover  $< 5\%$ ) plots.

single *E. farinosa* hit out of the 121 point intercepts. However, on a later visit to the densely infested CAMP site that had the longest known infestation (29 years) following a wet winter in 2010, we found numerous *E. farinosa* seedlings growing in the interstitial gaps between *P. ciliare* plants, suggesting a more mesic precipitation regime may support coexistence, if only temporarily. The winter of 2010 (32.8 cm in over 5 months ending in April, 2010) was the wettest winter at this site since 1998 (41.9 cm) (WRCC 2011). Long-term monitoring is recommended to determine whether *E. farinosa* can coexist with *P. ciliare* in this habitat, but the apparent strong volatility of *E. farinosa* to *P. ciliare* during a slightly drier era preceding our field work bodes poorly for continued *E. farinosa* dominance in the presence of *P. ciliare*.

Linking succession-like patterns of ecosystem change associated with *P. ciliare* invasion with the spatial patterns of invasive spread suggests a spatial pattern of ecosystem transformation in which initial invasion by *P. ciliare* negatively affects succulents, shrubs, native grasses and forbs. Once *P. ciliare* becomes the dominant cover, it interacts with *P. microphylla* and other trees such that tree cover declines over time, possibly punctuated by drought years. The iconic *C. gigantea* may also be at risk through recruitment inhibition or juvenile mortality, a decline that would likely take the better part of a century to play out on account of their long life cycle. If we consider these results as a formula for succession, we can visualize the spatial pattern of ecosystem transformation as early-, mid- and late-stages of transformation by mapping the percent cover of *P. ciliare* and time since invasion, as in Fig. 4.

The spatial patterns and temporal dynamics of this transformation vary markedly from what would be expected from a fire-induced transformation. Whereas competition-induced transformation follows a successional path wherein weaker plants succumb early followed by progressively stronger plants, fire-induced transformation is immediate but unpredictable in space and time and is likely to be limited to non-existent in spatial extent until invasion has created large, well-connected areas of fine fuels capable of carrying fire across the landscape. Presently, bare mineral soil characterizes so much of uninvaded Arizona Upland landscapes that fires are extremely rare and limited in extent. The rare fires that have burned Sonoran Desert landscapes have been fuelled by annual invasive grasses such as *Bromus madritensis* var. *rubens* (Humphrey, 1974; McLaughlin & Bowers, 1982; Schmid & Rogers, 1988). Although fire regime changes are expected to play a major role in ecosystem transformation due to *P. ciliare* in the long-term, early post-invasion dynamics are dominated by competition, at least in the Arizona Upland where fires historically may have occurred as rarely as once every 250 years (Thomas, 1991).

## CONCLUSIONS

Invasion by *P. ciliare* leads to a successional transformation of open, diverse desert scrub to depauperate  $C_4$  grassland interspersed with few long-lived species that may not be able to self-replace in the presence of *P. ciliare*. Impacts on native

species are acute (e.g. immediate loss of *Encelia farinosa* and *Mammillaria grahammii*), chronic (e.g. slow decline of long-lived saguaros without recruitment) or somewhere in the middle (e.g. lagged decline of *Parkinsonia microphylla*). Both *P. ciliare* spread and ecosystem transformation occur at predictable rates. While the threat that invasive grasses pose to ecosystems and human safety is potentially serious, the ecological benefits of preventing fire or even postponing fire may be overstated, at least in the case of *P. ciliare* in the northern Sonoran Desert. By the time *P. ciliare* populations conducive to large desert fires have been reached, the long-invaded interiors of these buffelgrass patches may be largely devoid of native vegetation. *P. ciliare* is one example of a grass–fire cycle-inducing species whose competitive effects outweigh the effects posed by fire early on in the invasion process. Its moderate rate of spread delays landscape-scale connectivity of fine fuels in an otherwise fire-proof ecosystem while ensuring some level of ecosystem transformation has occurred before fire has the opportunity to transform this ecosystem. We expect that even after landscape-scale connectivity of fine fuels is reached, the relative impacts of competition will continue to increase deterministically in accordance with spread rates while fire represents an instantaneous yet uncertain outcome.

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