Scale dependent relationships between native plant diversity and the invasion of croftonweed (Eupatorium adenophorum) in southwest China

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Croftonweed is an invasive plant in southwest China. We examined the relationships between its invasion patterns and native plant diversity at different spatio-temporal scales. At the 25 m² scale, invasion success was negatively correlated with native plant diversity, indicating that resource availability might be the dominant factor regulating community invasibility. At the 400-m² scale, both negative and positive relationships were detected, possibly identifying a spatial scale threshold where extrinsic environmental factors became more important to community invasibility. At the vegetation province scale, variations in physical environment outweighed the importance of intrinsic biotic factors and positive relationships between diversity and invader success were found. Native plant diversity also inhibited croftonweed over the course of community succession and at the early stages of invasion at local spatial scales. However, the changing relationship might be an artifact of sampling at different spatial scales.

Nomenclature: Croftonweed, Eupatorium adenophorum Sprengel EUPAD.

Key words: Biodiversity, biological invasions, community succession, invasive species, spatio-temporal scale.

Materials and Methods

We analyzed native plant diversity and community invasibility relationships at five spatial scales ranging from 25 m² to 2.53 by 10¹¹ m² (Table 1) and over the course of community succession and invasion by croftonweed. Vegetation data was gathered at the local scale in 400-m² plots using a nested design (Table 2) in 2003 and 2004. At each site, three 20-by-20-m plots were randomly established in representative vegetation types as described in China Vegetation (Wu 1995), including low, middle, and high canopy densities (0–30%, 31–70%, and 71–100%; Parendes and Jones 2000). In each plot, three 5-by-5-m subplots were placed in alternate corners and at the plot center, and one 1-by-1-m sub-subplot was placed in the right lower corner of each 5-by-5-m subplot. Percent cover of each tree species in the overstory was visually estimated in the 20-by-20-m plots; cover and abundance of each shrub, including croftonweed, was estimated in the 5-by-5-m subplots; forb cover and abundance was estimated in the 1-by-1-m sub-subplots. Abundance refers to the visual estimation of the number of shrubs and forbs in each sample unit according to Braun-Blanquet’s five abundance classes (Li 1993). Longitude, latitude, elevation, slope and aspect data were recorded for each plot. Plant species that could not be identified in the field were collected and identified at the herbarium of the Institute of Botany, Chinese Academy of Sciences.

We combined data collected at the local scales to comprise vegetation data at the regional scales. Wu (1995) clas-
sified the vegetation districts of China into eight vegetation regions, 18 vegetation zones, and 85 vegetation provinces. The large-scale level in our study was comprised of two vegetation regions, three vegetation zones, and five vegetation provinces: Subtropical evergreen broad-leaved forest vegetation region (I); Central subtropical evergreen broad-leaved forest vegetation zone (IA); Central Yunnan plateau and basin, *Cyclobalanopsis glaucoides–Castanopsis–Pinus yunnanensis* forest vegetation province (IA-1); Sichuan and Yunnan Jinshajiang River gorge, *Pinus yunnanensis*-dry, hot valley vegetation province (IA-2); South subtropical monsoon evergreen broad-leaved forest vegetation zone (IB); Yunnan, Guizhou and Guangxi calcareous mountain, *Machilus pingii–Cyclobalanopsis glauca–Pinus yunnanensis var. tenuifolia* forest vegetation province (IB-1); Central and south Yunnan midmountain, *Castanopsis–Schima wallchii–Pinus khasya* forest vegetation province (IB-2); Tropical seasonal rainforest and rainforest vegetation region (II); North tropical seasonal rainforest and semievergreen seasonal rainforest vegetation zone (IIA); Southwest Yunnan valley and mountainous area, semi-evergreen seasonal rainforest vegetation province (IIA-1).

Sites in the vegetation provinces IA-1, IB-1 and IB-2, and IIA-1 were sampled from March 20 to April 20, 2003 and August 2004. Sites in province IA-2 were sampled from August 2–21, 2003.

All statistical analyses were conducted using Origin 6.0 (Microcal Software Inc. 1999) at P < 0.05 significance. We assessed the relationships between native plant richness, and cover and abundance of croftonweed using linear and second-order polynomial regression models at the local scales including 25 m² and 400 m². There were not enough data points to conduct the regression analysis at the large spatial scales of vegetation province, zone, and region. Instead, one-way analyses of variances (ANOVA) were used to analyze these data following arcsine square root transformation of all percentage values (Gelbard and Belnap 2003). To test the significant difference of cover, abundance of croftonweed, and native plant richness between successional stages, we used Fisher’s LSD for paired multiple comparison procedures.

### Results and Discussion

At the local scale of 25 m², linear regression analysis demonstrated significant negative correlations (P < 0.01) between native plant species richness and cover and abundance of croftonweed (Figures 1a and 1b). At the 400-m² scale, second-order polynomial regressions showed a negative relationship up to a critical threshold of native species richness.

### Table 1. The size (m²) and number of vegetation sampling units used to test the effects of spatial scale on the relationships between native plant diversity and community invasibility.

<table>
<thead>
<tr>
<th>Vegetation province</th>
<th>Location</th>
<th>Annual mean temperature</th>
<th>Extreme minimum temperature</th>
<th>Annual mean rainfall</th>
<th>Field sites</th>
<th>Plots</th>
<th>Subplots</th>
</tr>
</thead>
<tbody>
<tr>
<td>IA-2</td>
<td>25°30’–29°45’N, 100°–106°E</td>
<td>17</td>
<td>−3.4</td>
<td>1040</td>
<td>2</td>
<td>6</td>
<td>18</td>
</tr>
<tr>
<td>IB-1</td>
<td>23°–25°10’N, 101°30’–106°20’E</td>
<td>17–21</td>
<td>−4.4</td>
<td>900–1200</td>
<td>2</td>
<td>6</td>
<td>18</td>
</tr>
<tr>
<td>IB-2</td>
<td>22°30’–26°N, 98°10’–103°E</td>
<td>17–19</td>
<td>0</td>
<td>1200–1600</td>
<td>4</td>
<td>12</td>
<td>36</td>
</tr>
</tbody>
</table>

* The climatic and geographic data is from *China Vegetation* (Wu 1995) except for the location of IIA-1, which was calculated from our field investigation.
after which the relationship between croftonweed and native species richness turned positive. Forty-five percent of the variance of cover and 42% of the variance of abundance of croftonweed were explained by native plant richness (Figures 1c and 1d). At the vegetation province scale, cover \((F = 3.51, P = 0.01, \text{df} = 4)\) and abundance \((F = 4.24, P = 0.003, \text{df} = 4)\) of croftonweed were significantly different between vegetation provinces, and the cover of croftonweed was positively correlated with native plant richness (Figure 1e). At the zone and region level, there were no significant differences in cover and abundance of croftonweed between zones and regions \((P > 0.05)\), indicating that there was no relationship between the invasion of croftonweed and native plant richness at these spatial scales.

At the 25-m\(^2\) scale, the relationship between cover and abundance of croftonweed and native plant species richness was negative; i.e., the invasion by croftonweed decreased with increasing native plant species richness. Communities with high diversity appeared to be more resistant to invasion, supporting the hypothesis of Elton (1958). The physical environment such as climate was nearly homogeneous at the 25-m\(^2\) scale, and native plant diversity appeared to play an important role in regulating community invasibility. Competition for available resources might be the most important process influencing invasibility at this spatial scale. Higher species diversity could increase the probability of including species with traits similar to croftonweed and strongly competitive species, resulting in a greater utilization proportion of the potentially available resources (Hooper et al. 2005), thereby interfering with the ability for croftonweed to establish. Higher biodiversity might also enhance the probability that generalist natural enemies should occur (Hooper et al. 2005), but this mechanism might not necessarily inhibit invaders (Shea and Chesson 2002).

However, at the regional scale of vegetation province, the relationship between cover of croftonweed and native plant species richness was positive (Figure 1e), which indicated that species-rich communities were vulnerable to the invasion of croftonweed. At large spatial scales, variability in environmental factors such as soil fertility, propagule input, and disturbance regimes apparently outweighed the effects of species diversity on community invasibility (Hooper et al. 2005). Thus, extrinsic factors that contributed to spatial variation in the environment and promoted diversity in communities were more important to invader success than the direct effects of diversity (Foster et al. 2002). Temperature and moisture were the main climatic factors that influenced the occurrence of croftonweed (Zhao and Ma 1989); hence, microsites with favorable temperature and moisture conditions would likely favor the establishment of croftonweed. Interestingly, at the 400-m\(^2\) scale, both nega-
tive and positive relationships were found, possibly identifying a spatial scale threshold where species richness became less important and the physical environment more important in regulating invader success in communities. With increasing spatial scales, variability in the physical environment played a stronger role, whereas the role of competition and resource availability was weaker.

Among the three life forms (trees, shrubs, and forbs), the richness of the forb layer had the greatest correlation coefficient to croftonweed cover and abundance, which might indicate that the habitat requirements of croftonweed were similar to that of the forbs or that there was less competition between them as compared to shrubs and trees (Figure 2). Thus, diversity of the forb layer was least likely to inhibit croftonweed invasion. This result was consistent with the findings of Hobbs (1989) and Wiser et al. (1998), but contrasted with the view that communities tend to be more readily invaded by the invader representing a new morphological type (Johnstone 1986; Mooney and Drake 1989).

To determine how the relationship between native plant species richness and cover and abundance of croftonweed changes during succession, we simulated the community successional process using vegetation data from temporary 25-m² sample subplots in Kunming, Yunnan. The typical successional sequence in this district included two types: (1) from meadow to shrubland to coniferous forest to evergreen broad-leaved forest, and (2) from meadow to shrubland to coniferous forest to deciduous broad-leaved forest. Both the cover and abundance of croftonweed peaked at the shrubland stage in the deciduous and evergreen broad-leaved forest successional series (Figure 3). In the deciduous broad-leaved forest successional series, cover and abundance of croftonweed also showed a second peak at the climax forest stage (Figure 3b), which might indicate that this forest had a lower resistance to this invader than coniferous and evergreen broad-leaved forests. Greater light availability in the deciduous broad-leaved forests might contribute to this pattern. Changes in native species richness over successional stages were similar in both series and showed an inverse pattern to croftonweed invasion. The lowest diversity occurred at the shrubland stage, demonstrating the resistance of native plant diversity to croftonweed invasion over the course of community succession.

To examine the relationship between invader success and native species richness during the course of invasion, we studied vegetation data at the 400-m² scale from three sites (Xichang, Kunming, and Cangyuan) with different histories since time of invasion (Table 3). The time span was determined from the literature (Wang et al. 1994; Wu et al. 1984; Xue et al. 1979). At the early stages of invasion (~20 yr), abundance of croftonweed was significantly negatively correlated with total native plant species richness (P < 0.01), tree richness (P < 0.01), and shrub richness (P < 0.05). Cover of croftonweed also showed a negative correlation with tree richness (P < 0.05). After about 30 yr of invasion, native plant diversity was still negatively correlated within cover (P < 0.05) and abundance (P < 0.01) of croftonweed. After about 50 yr of invasion, the cover and abundance of croftonweed was not correlated with native plant diversity (P > 0.05). Based upon these results, native plant diversity apparently played an important role and enhanced community resistance to invasion at the early stage, but its effects diminished over the course of invasion. At the later stage (~50 yr), the invasion of croftonweed might be mainly correlated with abiotic factors, and the predictability of croftonweed occurrence from physical environment should improve (Wiser et al. 1998).

The inconsistency in the relationship between species
richness and community invisibility might undermine the general application of Elton’s hypothesis when making comparisons at multiple spatio-temporal scales (Stohlgren et al. 1999). The richness-invisibility relationship comparisons at different spatial scales demonstrated that intrinsic factors such as resource availability influence plant community invasion susceptibility at small spatial scales, and extrinsic factors such as physical environment influence plant community invisibility at larger scales. However, the changing relationship might be an artifact of sampling at different spatial scales. At local spatial scales, the ability to detect sites susceptible to invasion is diminished and the effects of biotic resistance to invasion are better detected. At regional spatial scales, the ability to detect habitable sites is improved. Temporal changes in species richness-invasion relationships were examined at small spatial scales and clearly showed the role of species diversity on invader success. The change in the relationship over time suggests that intrinsic factors such as plant competition are very important during the early stages of invasion. However, at later stages, environmental factors become more important. These results indicate the importance of identifying the stage of invasion relative to time (e.g., early, mid, or late stages) when studying invasion biology.

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