Testing the Shifting Persistence Niche Concept: Plant Resprouting along Gradients of Disturbance

Peter J. Clarke,1,∗ Dorothy M. Bell,1,∗ and Michael J. Lawes2,†

1. Botany, School of Environmental and Rural Sciences, The University of New England, Armidale, New South Wales 2351, Australia; 2. Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory 0909, Australia

Submitted August 8, 2014; Accepted December 8, 2014; Electronically published April 16, 2015

Online enhancement: appendix.

Abstract: Plant resprouting after disturbance confers community resilience because individuals persist through trade-offs in resources for buds versus those required to produce seeds. However, repeated disturbance may deplete bud banks, and population persistence may become increasingly reliant on regeneration from seed. Theory predicts a shift in community assemblage from species with a strategy of persistence by resprouting (persistence niche) to one of regeneration from seed (regeneration niche) as the disturbance frequency increases. We tested, for the first time, the shifting persistence niche concept in a model system at local and regional community scales using a phylogenetically diverse floristic assemblage. Persistence traits of vascular plants were modeled as a function of dry-down frequency in wetlands. Resprouting species occupying the persistence niche were more common in stable wetlands than in those more frequently disturbed by dry downs. The patterns of resprouting species in standing vegetation and in seed banks provide strong support for the shifting persistence niche model involving trade-offs between resprouting (clonality) and sexual reproduction.

Keywords: clonality, disturbance, ruderals, semelparity, trade-offs, wetlands.

Introduction

The modular nature of plants enables resprouting after disturbance; this ability has profound ecological consequences because of its effect as a functional trait on community assembly (Clarke et al. 2010). Resprouting response varies with growth form along gradients of disturbance (Bellingham and Sparrow 2000; Bond and Midgley 2001; Lamont et al. 2011) and provides a functional basis for predicting vegetation patterns. This relationship between resprouting ability and disturbance regime has stimulated the notion of a unified model of plant life history that applies across a range of plant communities (Sparrow and Bellingham 2001). In disturbance-prone environments, where plant deaths could cause demographic bottlenecks, resprouting from dormant buds maintains plant populations and therefore guarantees persistence (Bond and Midgley 2001; Ackerly 2003; Falster and Westoby 2005). These populations give rise to communities and ecosystems that are resilient to severe biomass-depleting disturbances such as drought, storm, and fire where individuals persist through resprouting (Clarke et al. 2013). Nevertheless, the ability of populations to resprout is ultimately constrained by finite bud banks, by how this allocation of resources is protected, and by carbohydrate resources for regrowth and can be depleted by repeated disturbance (Lawes and Clarke 2011; Clarke et al. 2013).

There is now strong empirical evidence of a trade-off between resource allocation for persistence (resprouting) and resource allocation for regeneration by seeding in response to disturbance (see review by Clarke et al. 2013). Species killed by disturbances have carbon allocation patterns that favor rapid growth and reproduction at the expense of storage; these occupy the regeneration niche. In contrast, those species that resprout occupy the persistence niche and allocate more resources to storage, protection, and bud banks (e.g., Vesk and Westoby 2004; Knox and Clarke 2005) and fewer resources to seed-based regeneration (Clarke et al. 2013). Combinations of these two strategies theoretically occur across disturbance gradients that are scaled to resource availability (Iwasa and Kubo 1997; Bellingham and Sparrow 2000; Chong et al. 2013; fig. 1). Hence, rising disturbance frequency results in increased selection for resprouting or stress-tolerant species under similar levels of productivity (light, nutrients, and water availability; Bellingham and Sparrow 2000). However, when disturbance frequency continues to increase, selection decreases for resprouting because buds cannot be replenished between short disturbance intervals. Concurrently, selection for seed-based regeneration increases, and resprouters decline (fig. 1). In fire-prone ecosystems, escalating fire frequency eliminates seed-based regeneration in nonsprouters, and resprouters dominate (Pausas 2001; Clarke and Dorji 2008; Nano and
but if short-interval fires continue, ephemerals dominate, resulting in a hump-shaped resprouting response at regional scales (Chong et al. 2013). Resprouting is also a successful ecological strategy in flood-prone environments where increasing disturbance intensity can drive resprouting and increasing clonality within species (Chong et al. 2013).

Escalating disturbance constrains the ability of plants to maintain a bud bank and remobilize nonstructural carbohydrates, especially when growing seasons are limited and plants lack woody storage capacity. These environments favor seedling success and adult mortality and select for semelparity over iteroparity (Charnov and Schaffer 1973). At this upper end of the disturbance spectrum, seed-based regeneration rather than bud bank reiteration should be favored, resulting in a reversal in resprouting selection (i.e., a shift from resource conservation to acquisition; Bellingham and Sparrow 2000; see shift over the hump in fig. 1). Thus, under frequent disturbance, herbaceous growth forms are favored over woody growth forms, and there is a predicted shift toward species that maintain a seed bank or rely on wind-dispersed seeds (Bellingham and Sparrow 2000; fig. 1). Such contrasting life-history traits are well known across growth forms (Grime 1977), but a predicted reversal in community assembly has not been empirically tested.

A model natural system for testing the shift in the persistence niche is one where resources for growth (light and nutrients) are in free supply but where disturbance interrupts supply and kills the units of resource acquisition (buds and storage) rather than forces plastic adjustment. Fire-prone communities are one such system, but fire frequency is constrained by biomass production, which self-limits disturbance frequency. In contrast, herbaceous wetlands are often subject to a disturbance (climate-driven drying regimes) that is not self-limiting but kills aboveground buds and storage. In addition, trade-offs for light acquisition are not strong because of the height-growth constraint of herbaceous growth forms. Instead, a clear distinction can be made between herbaceous species that resprout after disturbance and those that are killed by drying disturbance and rely on sexual reproduction. In wetlands, most resprouters appear to be clonal; new growth results from the formation of shoots from bud banks in stolons, rhizomes, tubers, and other meristematic tissue in plant fragments (Klimošová and Klimeš 2007; Sosnová et al. 2010), but these species are not developmentally constrained since nonresprouters are found in most family lineages. Furthermore, there is some evidence that disturbance-mediated resprouting influences allocation trade-offs between seed and growth in wetland plants (Watson 1984; Willby et al. 2000; Dorken et al. 2004). Hence, the hydrological regime of wetlands provides an ideal framework to identify how disturbance structures plant communities.

We predict wetland community assemblage reversal from a strategy of persistence (resprouting) to one of regeneration (nonresprouting) as the disturbance frequency of drying increases, driven by wetland hydrology. We test whether the shifting persistence niche concept operates at local and regional community scales and whether the resprouting versus nonresprouting trade-off is reflected in seed bank composition. In short, we predict a community shift driven by stress tolerance from an assemblage where the persistence niche is favored (fig. 1, peak in resprouting) to one where the regeneration niche becomes dominant (fig. 1, decline in resprouting).

Methods

Study Sites and Sampling

To address whether resprouting is linked to disturbance (see "Disturbance Regime"), we recorded the life-history attributes of all vascular plant species in freshwater wetlands
across long-term wetting and drying regimes in southeastern Australia. The families and genera of these species are generally widespread within Australia. At the regional scale (bioclimatic zone), we measured species resprouting attributes in three freshwater wetland assemblages at the same latitude but with differing wetting and drying regimes: (i) coastal, low drying frequency; (ii) upland, intermediate drying frequency; and (iii) inland wetlands, high drying frequency (tables 1, A1; tables A1–A3 are available online; see "Disturbance Regime"). For each regional assemblage, 4–5 independent wetlands were sampled in 7–20 quadrats (0.01–0.1 ha; table 1).

At the local scale, we examined patterns of resprouting within five upland wetlands across disturbance (topographic) gradients that give rise to variations in dry-down frequencies but that have neither extreme drying down (inland wetlands) nor constancy in inundation (coastal wetlands). Hence, the local effects of modes of regeneration across a gradient from the center of the wetland to the perimeter can be assessed only in the upland wetlands. Within the upland wetlands, three disturbance (depth) levels were sampled: (i) wetland edge, high drying frequency; (ii) slope, intermediate drying frequency; and (iii) basin, low drying frequency (see disturbance regime; table A2). Five independent upland wetlands were sampled nine times over 2 years. Within each location (edge, slope, or basin) at each time, four quadrat samples (0.5 m²) measured species abundance (frequency score) in seven nested subsamples (see Morrison et al. 1995 for nested quadrat method). This repeated sampling takes into account shifts in community dominance in relation to water depth and wave action (Yen and Myerscough 1989).

**Soil Seed Bank Sampling**

In the five upland wetlands, we also sampled soil seed bank composition in the three dry-down disturbance regimes (edge, slope, and basin, as per standing vegetation) to test the potential allocation trade-off to resprouting versus seed production across the dry-down gradient. The frequency of species with seeds in the soil-stored seed bank was compared among the three depth locations (edge, slope, and basin) in five upland wetlands with four subsamples within each of three replicate sediment cores (4 × 4 × 13 cm³). Cores were sampled from depth locations adjacent to those used for vegetation sampling. Samples were air-dried and then wetted and sorted using a series of sieves (2 mm, 1 mm, 500 μm, and 250 μm), where all diaspores (seeds, fruits, megaspores, and turions) were identified and species presence/absence recorded. These species were then grouped into their functional classes for frequency analyses (see species attributes in table 3).

**Disturbance Regime**

Disturbance regime was measured in terms of drying regimes of freshwater wetlands that kill aboveground biomass of wetland plants. These occur in Australia because of the pronounced Southern Oscillation climate effect on rainfall (Allen et al. 1996). Dry downs lasting more than 6 months result in the removal of aboveground biomass, and wetland drying is more frequent than disturbances such as fire and more intense than localized waterbird herbivory. In the absence of long-term records of wetland drying in the regional assemblages, a measure indicating the likely frequency and duration of drying-out periods was developed from long-term Australian Bureau of Meteorology climate data for nearby weather stations: coastal (Coffs Harbour), upland (Guyra), and inland (Narrabri; table A3). The length of the climate record varied from 40 years at Narrabri to 60 years at Coffs Harbour. Monthly mean temperatures were calculated from daily minimum and maximum temperatures, and potential evaporation was calcu-

---

### Table 1: Assemblage characteristics of sampled wetlands in southeastern Australia

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Coastal</th>
<th>Upland</th>
<th>Inland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Formation type</td>
<td>Coastal freshwater lagoons</td>
<td>Montane lakes</td>
<td>Pilliga wetlands</td>
</tr>
<tr>
<td>Wet/dry frequency</td>
<td>Low</td>
<td>Intermediate</td>
<td>High</td>
</tr>
<tr>
<td>Geomorphology</td>
<td>Sand plain depressions</td>
<td>Deflation basins</td>
<td>Relict drainage line depressions</td>
</tr>
<tr>
<td>Latitude/longitude</td>
<td>30°18’S/153°08’E</td>
<td>30°05’S/151°46’E</td>
<td>30°30’S/149°22’E</td>
</tr>
<tr>
<td>No. locations sampled</td>
<td>4</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>No. quadrats within locations</td>
<td>16, 20, 20, 20</td>
<td>12, 12, 12, 12, 12, 12</td>
<td>15, 11, 19, 7</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>10</td>
<td>950</td>
<td>350</td>
</tr>
<tr>
<td>Mean annual rainfall (mm)</td>
<td>1.346</td>
<td>880</td>
<td>663</td>
</tr>
<tr>
<td>Mean duration of rainfall deficit (months)</td>
<td>1.62</td>
<td>1.67</td>
<td>3.32</td>
</tr>
<tr>
<td>Probability of deficit period ≥4 months</td>
<td>1.41</td>
<td>2.44</td>
<td>22.58</td>
</tr>
<tr>
<td>Mean annual days of rain</td>
<td>100</td>
<td>82</td>
<td>38</td>
</tr>
<tr>
<td>Maximum/minimum temperature (°C)</td>
<td>13.9–22.9</td>
<td>5.3–17.9</td>
<td>11.7–26.5</td>
</tr>
</tbody>
</table>
lated using the Thornthwaite (1948) method. Subtracting monthly rainfall from potential evaporation provides monthly time series for rainfall deficit in each region. From these, we calculated frequency distributions of monthly deficit durations (i.e., the duration of periods of consecutive monthly rainfall deficits). Two descriptive statistics for these distributions are reported: the mean duration of periods of consecutive monthly rainfall deficits and the probability of a deficit period exceeding 4 months (table 1). Drydown is infrequent in the coastal freshwater lagoons, occurring only with major drought at infrequent decadal intervals (table 1); however, shifts in community dominance occur in relation to water depth (Yen and Myerscough 1989).

The upland montane lakes wetlands have more frequent dry downs than the coastal lagoons (table 1); their water levels are maintained mostly by groundwater and surface runoff from small catchments in a region with lower and more variable rainfall (Bell et al. 2008). Their margins regularly experience dry down within and between seasons, but their deflation basins will be more likely to dry down at decadal intervals with fluctuations in the Southern Oscillation index (Allan et al. 1996). The inland wetlands occur in depressions with small catchments but are prone to more rapid and frequent drying (table 1) because of the higher evapotranspiration that occurs over summer in a region with high summer temperatures and lower and more unpredictable rainfall (Bell et al. 2012). Wave action is a minor disturbance component and is unlikely to influence re-sprouting in any of these wetlands as it does not completely defoliate plants. Fire disturbance is very rare in these wetlands, and ungulate grazing is excluded from these wetlands.

At the local scale, dry down within the upland lake sample locations (edge, slope, and basin) was measured directly over 4 years of monitoring on 10 occasions where water depth was recorded in each location (edge, slope, and basin) across five independent wetlands (fig. A1, available online). The proportion of months where there was no water above sediment was summed across all five lakes for each location to give a frequency index of dry down (edge = 0.46; slope = 0.20; basin = 0.10). Water-depth measurements show the contrasting drying frequency at the three depth levels sampled in the upland lagoon (fig. A1). Drying frequency is primarily related to topography as the upland wetlands are groundwater and overland fed.

**Species Attributes**

We compiled lists of taxa and their life-history attributes for the sampled freshwater wetland assemblages at a sub-tropical latitude in southeastern Australia (tables 2, A1, A2; see Keith 2004). The structure of these wetlands varies from aquatic herb fields to sedgelands, and the major growth forms—submerged, emergent, free floating, and ruderals—are present in all systems (Beadle 1981; Keith 2004). Sampling at the upper edge of the upland wetland was located so it was submerged for part of the year but did not include species that also occur in terrestrial environments. A total of 49 plant families were recorded, of which only three families were unique to one region; species in these families were omitted from trait analyses. Four families (Cyperaceae, Haloragaceae, Juncaceae, and Menyanthaceae) had congeners across all regions (table A1).

### Table 2: Regional-scale summary of species proportions for aquatic growth forms, total resprouters, and drying response groups

<table>
<thead>
<tr>
<th>Type</th>
<th>Coastal (n = 54)</th>
<th>Upland (n = 42)</th>
<th>Inland (n = 72)</th>
<th>F-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aquatic herbaceous growth forms:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Submerged (Sb; %)</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Emergent (Em; %)</td>
<td>81</td>
<td>77</td>
<td>32</td>
<td></td>
</tr>
<tr>
<td>Free floating (FF; %)</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Ruderal (Ru; %)</td>
<td>9</td>
<td>21</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td>Resprouters (R+; %)</td>
<td>85</td>
<td>70</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td>Resprouter long lived (R+L; %)</td>
<td>74</td>
<td>70</td>
<td>32</td>
<td></td>
</tr>
<tr>
<td>Resprouter short lived (R+S; %)</td>
<td>11</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Nonresprouter long lived (R−L; %)</td>
<td>11</td>
<td>11</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Nonresprouter short lived (R−S; %)</td>
<td>4</td>
<td>19</td>
<td>58</td>
<td></td>
</tr>
</tbody>
</table>

Note: Generalized linear model (logit link function) results for number of species with trait, with total number of species in replicate samples as the binomial n. F-test denominator calculated for Pearson’s χ².

* Note that only 5% of ruderals were neophytes. NS = not significant.

b Nonconvergence in model.

* P > .25.

** P < .001.

This content downloaded from 23.235.32.0 on Wed, 7 Oct 2015 01:50:46 AM
All use subject to JSTOR Terms and Conditions
For two of the coastal wetland sites, lists of species were compiled from published descriptions that used quadrat sampling (5 × 5 m; Griffith et al. 2003; Griffith and Wilson 2008), while we compiled other lists from quadrat sampling (2 × 2 m) of herbaceous wetland communities. We classified all herbaceous species in our sampling plots into four broad categories that were combinations of resprouter versus nonresprouter and long lived versus short lived, based on field observations and/or fl ora records. Species were designated as resprouter if rhizomes, stolons, tillers, or rooting at nodes or from fragments were reported or observed and were designated as short lived if reported as being annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2). A small number of species that are known to be annual or short lived (see species summary attributes in table 2).
three depth classes (table 3), with the system being dominated by emergent species regardless of the depth class (table 3). While more resprouting species were recorded in the basin locations, the proportion of resprouters to nonresprouters was not significantly different among depths (table 3; power $p = 0.38 - 0.52$). Nevertheless, when the relative abundances (frequency scores) of resprouting species summed over time were compared among depths, there was a significant difference (table 4), with the mean relative abundance of resprouters being higher in the basin (97.1%) than on the slopes (80.6%) and on the edge (83.0%; table 4).

Within the upland wetlands, there were significant effects of depth and plots for the frequency of species with soil-stored seed (table 4). Overall, there was a higher proportion of resprouting species recorded in the seed bank of the basin of upland wetlands than on the edges. Cumulative frequency scores (extant vegetation) regressed against summed frequencies (seed bank) resulted in a steeper slope for the line of best fit for nonresprouters (slope = 0.143; $R^2 = 0.71; P < .001$) compared to resprouters (slope = 0.085; $R^2 = 0.85; P < .001$).

### Discussion

**Is Persistence-Niche Occupancy Mediated by Disturbance?**

We found that the proportion of resprouting species decreased with increasing disturbance frequency at two spa-

### Table 3: Local-scale summary of species (richness) proportions for aquatic growth forms, resprouters, and drying response groups for a single sampling occasion (summer 1995)

<table>
<thead>
<tr>
<th>Type</th>
<th>Local assemblage locations</th>
<th>Edge (n = 53)</th>
<th>Slope (n = 39)</th>
<th>Basin (n = 42)</th>
<th>F-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aquatic herbaceous growth forms:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Submerged (Sb; %)</td>
<td></td>
<td>2</td>
<td>5</td>
<td>12</td>
<td>$F_{2.12} = 1.71^{NS}$</td>
</tr>
<tr>
<td>Emergent (Em; %)</td>
<td></td>
<td>72</td>
<td>69</td>
<td>69</td>
<td>$F_{2.12} = .37^{NS}$</td>
</tr>
<tr>
<td>Free floating (Ff; %)</td>
<td></td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>$F_{2.12} = 1.49^{NS}$</td>
</tr>
<tr>
<td>Ruderal (Ru; %)</td>
<td></td>
<td>25</td>
<td>23</td>
<td>17</td>
<td>$F_{2.12} = .44^{NS}$</td>
</tr>
<tr>
<td>Resprouters (R+; %)</td>
<td></td>
<td>64</td>
<td>69</td>
<td>74</td>
<td>$F_{2.12} = .34^{NS}$</td>
</tr>
<tr>
<td>Resprouter long lived (R+L; %)</td>
<td></td>
<td>60</td>
<td>56</td>
<td>60</td>
<td>$F_{2.12} = .11^{NS}$</td>
</tr>
<tr>
<td>Resprouter short lived (R+S; %)</td>
<td></td>
<td>4</td>
<td>13</td>
<td>14</td>
<td>$F_{2.12} = 1.07^{NS}$</td>
</tr>
<tr>
<td>Nonresprouter long lived (R–L; %)</td>
<td></td>
<td>13</td>
<td>13</td>
<td>10</td>
<td>$F_{2.12} = 1.61^{NS}$</td>
</tr>
<tr>
<td>Nonresprouter short lived (R–S; %)</td>
<td></td>
<td>23</td>
<td>18</td>
<td>17</td>
<td>$F_{2.12} = .11^{NS}$</td>
</tr>
</tbody>
</table>

Note: Generalized linear model (logit link function) results for a number of species with trait, with total number of species in replicate samples as a binomial n. F-test denominator calculated for Pearson’s $\chi^2$. NS = not significant.

### Table 4: Local-scale results for abundance (frequency score) of resprouter species proportions over time (1994–1998) and seed bank species (% total richness) for resprouters

<table>
<thead>
<tr>
<th>Variable</th>
<th>Local site locations (depth)</th>
<th>Edge</th>
<th>Slope</th>
<th>Basin</th>
<th>F-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean abundance of resprouter species (%)</td>
<td></td>
<td>83.0</td>
<td>80.6</td>
<td>97.1</td>
<td>$F_{4.44} = 9.68^{**}$</td>
</tr>
<tr>
<td>Depth</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>$F_{4.44} = 5.50^{**}$</td>
</tr>
<tr>
<td>Plots (depth)</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>$F_{4.44} = .63^{NS}$</td>
</tr>
<tr>
<td>Subsamples (plots [depth])</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>$F_{4.44} = 3.40^{NS}$</td>
</tr>
<tr>
<td>Mean resprouter species in seed bank (%)</td>
<td></td>
<td>73.1</td>
<td>82.5</td>
<td>83.8</td>
<td>$F_{4.50} = 11.16^{**}$</td>
</tr>
<tr>
<td>Depth</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>$F_{4.50} = 6.12^{**}$</td>
</tr>
<tr>
<td>Plots (depth)</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>$F_{4.50} = .39^{NS}$</td>
</tr>
<tr>
<td>Samples (plots [depth])</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>$F_{4.50} = .39^{NS}$</td>
</tr>
</tbody>
</table>

Note: Generalized linear model (GLM; identity link function) results for abundance of resprouter species with nested spatial factor effects. GLM (logit link function) results are shown for the proportion of resprouter species in the seed bank with nested spatial factor effects. NS = not significant.

** ** P < .001.
and shoots for growth and storage. Our sprouting. Subsequently, new ramets quickly develop roots of nonstructural carbohydrates are needed to fund initial re-

professional experience is no guarantee of persistence since some clonal species variability requires testing.

Clonality is the predominant mechanism for occupying the persistence niche in these communities, although clonality is no guarantee of persistence since some clonal species are ephemeral (table 2). Clonality in perennial species has an advantage for persistence because only a small amount of nonstructural carbohydrates are needed to fund initial re-

In these wetlands, no explicit test of the trade-off between seed production and persistence by resprouting appears to exist at least in the upland wetlands. This trade-off is manifested in the clear reduction in viable seed bank numbers between the disturbance-prone edges and the more stable deep basins of upland wetlands found by Brock (2011). We also found more seeds of nonsprouting species in disturbance-prone edges where nonsprouters are present, although the presence of nonviable seed could influence this trend. Increased abundances of nonsprouting species also corresponded to a greater accumulation (steeper slope) of nonsprouting seeds compared to that of resprouter abundances and seed bank. While we did not sample the abundance of seeds be-

Are Trade-offs in Resprouting Manifested in Seed Banks?

For short-lived and semelparous species, investment in sexual reproduction is mandatory if populations are to be maintained through extreme fluctuations. Similarly, for perennial species that lack resprouting capacity, there is a well-

known trade-off between survival and sexual reproduction, with greater allocation to reproduction in congeners that are nonsprouters (Lawes and Clarke 2011). These trade-offs more generally align with the loss of sex syndrome in some clonal plants (Vallejo-Marin et al. 2010) and the frequency of monoclonal populations in aquatic herbs (Silvertown 2008). Hence, seed bank composition should reflect this trade-off at community levels (e.g., Clarke and Dorji 2008). In these wetlands, no explicit test of the trade-off was measured at the species/congenor level, although at the community level, the trade-off between seed production and persistence by resprouting appears to exist at least in the upland wetlands. This trade-off is manifested in the clear reduction in viable seed bank numbers between the disturbance-prone edges and the more stable deep basins of upland wetlands found by Brock (2011). We also found more seeds of nonsprouting species in disturbance-prone edges where nonsprouters are present, although the presence of nonviable seed could influence this trend. Increased abundances of nonsprouting species also corresponded to a greater accumulation (steeper slope) of nonsprouting seeds compared to that of resprouter abundances and seed bank. While we did not sample the abundance of seeds be-
between regions, we noted the large numbers of seedlings in more frequently disturbed wetlands than in the least disturbed wetlands. Quantifying the abundance, species composition, and viability of seeds in seed banks is a critical issue for understanding trade-offs in allocation to reproduction that remain to be resolved. Seedling survival is likely to be high in wetland systems undergoing fluctuations rather than those in dry down because the fundamental conditions for growth are enhanced by the lack of shading, the free availability of water, and the high nutrient status of wetland sediments.

Disparities between the composition of extant plant communities and their seed banks are often noted in both terrestrial and wetland community studies (see the review by Hopfensperger 2007). Leck (1989) noted a putative link between clonality and low seed production of a dominant wetland species, but the idea that the persistence niche drives the difference between the overt plant community and the covert (seed bank) plant community has not been strongly developed in either wetland or terrestrial community theory. This is despite the conceptual framework provided by the storage effect, where persistence during unfavorable times requires a life stage that withstands unfavorable conditions (Warner and Chesson 1985). By demonstrating that there is a clear link between disturbance frequency and the resprouting composition of wetland communities, we suggest that the shifting persistence niche concept has utility in both terrestrial and aquatic systems.

In conclusion, the link between patterns of community assembly to trade-offs in species performance for different ecological functions underpins the debate about niche theory versus neutral models (Knetel and Chase 2004). We have suggested that trade-offs in resprouting versus seeding can influence the ability of species to occupy the persistence niche primarily because plants are limited in their ability to resprout after repeated and frequent disturbance in wetlands. This result suggests that both local community- and regional community-level coexistence in disturbance-driven communities is fundamentally mediated by resprouting ability, after which other trade-off trade-offs such as competitive ability and predator tolerance influence community assembly.

Acknowledgments

We thank I. Reeve for developing a measure of the likely frequency and duration of dry down from long-term climatological data. J. Hunter highlighted the existence of the ephemeral wetlands in the Pilliga Outwash, and J. Burne assisted in the surveys of the upland wetlands. NSW National Parks and Wildlife Service allowed access to survey wetland communities. The ARC-NZ Research Network for Vegetation Function stimulated research into resprouting and the persistence niche.

In memoriam. To the memory of Peter J. Clarke, whose enthusiasm for botany, particularly his contribution to the ecology of resprouting and the persistence niche, inspired all of his colleagues. And to the memory of Dorothy M. Bell, who was a PhD student in Peter Clarke’s lab.

Literature Cited


