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Testing the Shifting Persistence Niche Concept

Plant Resprouting along Gradients of Disturbance

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The University of Chicago

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

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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
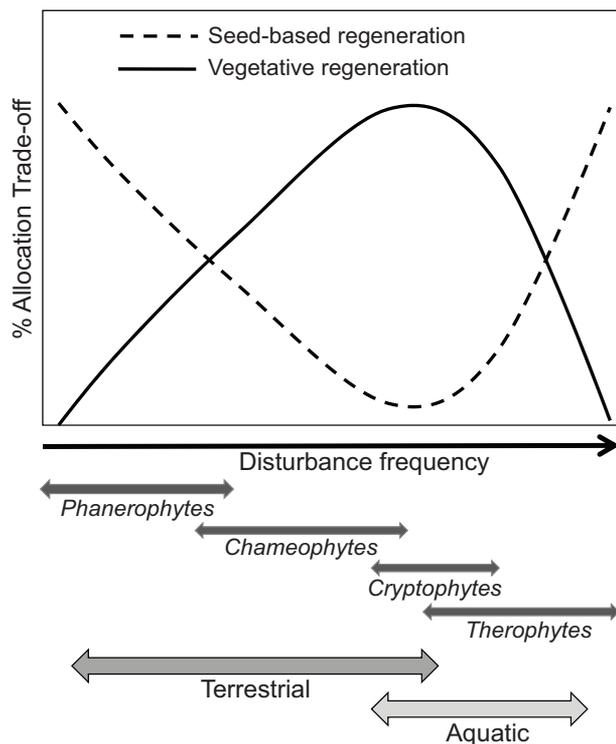
Figure 1: Allocation trade-off model proposed by Bellingham and Sparrow (2000). The model predicts that as disturbance frequency increases, allocation to resprouting should increase until the frequency of disturbance reduces the bud bank. Thereafter, seed-based regeneration becomes more common. Aquatic communities often have high disturbance frequencies; hence, these systems are ideal for testing the extreme end of the model where the persistence niche (sensu Bond and Midgley 2001) may not occur.

Clarke 2011); but if short-interval fires continue, ephemerals dominate, resulting in a hump-shaped resprouting response at regional scales (fig. 1; see also Clarke 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 pre-

dicted 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 (Klimešová 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 ($4 \times 4 \times 13$ 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

	Assemblage		
Characteristic	Coastal	Upland	Inland
Formation type	Coastal freshwater lagoons	Montane lakes	Pilliga wetlands
Wet/dry frequency	Low	Intermediate	High
Geomorphology	Sand plain depressions	Deflation basins	Relict drainage line depressions
Latitude/longitude	30°18′S/153°08′E	30°05′S/151°46′E	30°30′S/149°22′E
No. locations sampled	4	5	4
No. quadrats within locations	16, 20, 20, 20	12, 12, 12, 12, 12	15, 11, 19, 7
Altitude (m)	10	950	350
Mean annual rainfall (mm)	1,346	880	663
Mean duration of rainfall deficit (months)	1.62	1.67	3.32
Probability of deficit period ≥4 months	1.41	2.44	22.58
Mean annual days of rain	100	82	38
Maximum/minimum temperature (°C)	13.9–22.9	5.3–17.9	11.7–26.5

lated using the Thornthwaite (1948) method. Subtracting monthly rainfall from potential evaporation provided 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). Dry down 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 resprouting 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 subtropical 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

	Regional assemblage locations			
Type	Coastal ($n = 54$)	Upland ($n = 42$)	Inland ($n = 72$)	F-test
Aquatic herbaceous growth forms:				
Submerged (Sb; %)	4	2	3	$F_{2,10} = 1.26^{*,NS}$
Emergent (Em; %)	81	77	32	$F_{2,10} = 27.74^{**}$
Free floating (Ff; %)	6	0	0	$F_{2,10} = 94.15^{**}$
Ruderal (Ru; %)[a]	9	21	64	$F_{2,10} = 43.00^{**,b}$
Resprouters (R+; %)	85	70	33	$F_{2,10} = 32.52^{**}$
Resprouter long lived (R+L; %)	74	70	32	$F_{2,10} = 23.82^{**}$
Resprouter short lived (R+S; %)	11	0	1	$F_{2,10} = 29.63^{**}$
Nonresprouter long lived (R−L; %)	11	11	8	$F_{2,10} = .52^{*,b,NS}$
Nonresprouter short lived (R−S; %)	4	19	58	$F_{2,10} = 57.6^{**}$

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 χ^2.

[a] Note that only 5% of ruderals were neophytes. NS = not significant.

[b] Nonconvergence in model.

* $P > .25$.

** $P < .001$.

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 flora 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 resprout from basal or root meristems after grazing or fire but not wetland drying were also recorded. All of these species were nonclonal and attributed to nonresprouter long-lived species; in the narrower context, they are nonresprouters because they are not damaged by wetland drying per se. All clonal persistent species had leaves and culms that senesce during dry down but on rewetting had persistent axillary and apical buds that are the source for new growth.

Statistical Analyses

We separately fitted the proportion of species in (1) four growth form/functional classes (submerged, emergent, free floating, and ruderal) and (2) four resprouting classes (resprouter long lived, resprouter short lived, nonresprouter long lived, and nonresprouter short lived) as response variables to the three regional levels of disturbance (coastal, upland, and inland) using generalized linear model (GLM) analysis by binomial proportions with a logit link function. The independent locations (4–5) within sites were used as replicates, and in each site the binomial n was the total number of species present, adjusted for family presence across all regions. The F-test denominator was calculated from Pearson's χ^2 using GLMstat software after the residuals were examined. For a single local-scale sampling occasion (summer 1995), we also fitted the proportion of species in the same functional classes to the three local levels of disturbance (edge, slope, and basin) using GLM with a logit link function and with the five upland wetlands as replicates.

In addition, we examined differences in the relative abundance over time of resprouters versus nonresprouters in the three depth locations in the upland wetland sites (edge, slope, and basin) using a nested generalized linear mixed model (GLMM; identity link function). The fixed factors in the model were depth (edge, slope, and basin), and the random nested factors were plots ($n = 5$) nested in depth and subsamples ($n = 4$) nested in plot and depth. The response variable abundance measurements were the cumulative frequency scores from nine sampling occasions over 2 years when wetlands ranged from relatively dry to wet.

The frequency of species with seeds in the soil-stored seed bank was also compared among the three depth locations (edge, slope, and basin) in the upland wetland assemblage using a GLMM (logit link function) with a binomial error structure where the binomial n was the number of soil sediment samples taken. The fixed factors in the model were depth (edge, slope, and basin), and the random nested effects were plots ($n = 5$) nested in depth and subsamples ($n = 4$) nested in plots. The response variable resprouter seed bank measurements were species frequencies in seed banks assessed from species presence/absence in three replicate sediment cores. The fixed factors in the model were depth (edge, slope, and basin), and the random nested effects were plots ($n = 5$) nested in depth and subsamples ($n = 4$) nested in plots.

To test whether there was, as predicted, a trade-off between resources allocated to persistence versus regeneration, we regressed cumulative frequency scores (extant vegetation) against summed frequencies (seed bank) for resprouters and nonresprouters separately. A greater accumulation of nonresprouter seeds in the seed bank with increasing species abundance in the extant vegetation should result in a steeper fitted function.

Results

The total number of species recorded was highest in the inland wetlands (72) and lowest in the upland wetlands (42; table 2), with a total of 49 families present, of which 46 occur across all three wetland assemblages. The proportion of species in the growth-form classes varied significantly among the three study areas, apart from the submerged proportion (table 2). Larger proportions of ruderal species were recorded in the inland wetlands, and conversely, larger proportions of emergent species were found in the coastal and upland wetlands (table 2). Consequently, there was also a significantly higher proportion of resprouter species in the coastal and upland wetlands (85%) than in the inland wetlands (33%; table 2). This was mirrored in the increasing proportion of long-lived resprouter species where the proportion was highest in the coastal wetlands (74%) but lowest in the inland wetlands (32%; table 2). Conversely, the proportion of nonresprouter and short-lived (i.e., dry-down nonresprouters) species was highest in the inland wetlands (58%) and lowest in the coastal wetland sample sites (4%; table 2).

At the local scale, the total number of species ranged from 39 species on the slope to 53 species on the edge of the upland wetlands (table 3). The proportion of species in growth-form classes did not vary significantly among the

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)

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

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 χ^2. NS = not significant.

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 = 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 pro-

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

| | Local site locations (depth) | | | |
Variable	Edge	Slope	Basin	F-test
Mean abundance of resprouter species (%)	83.0	80.6	97.1	...
Depth	...	...	...	$F_{2,44} = 9.68^{**}$
Plots (depth)	...	...	...	$F_{4,44} = 5.50^{**}$
Subsamples (plots [depth])	...	...	...	$F_{3,44} = .63^{NS}$
Mean resprouter species in seed bank (%)	73.1	82.5	83.8	...
Depth	...	...	...	$F_{2,50} = 11.16^{**}$
Plots (depth)	...	...	...	$F_{4,50} = 6.12^{**}$
Samples (plots [depth])	...	...	...	$F_{3,50} = .39^{NS}$

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.

** $P < .001$.

tial scales. At the landscape scale, more species occupied the persistence niche (85%) in coastal communities; these are less prone to dry-down disturbance than inland communities. The highly fluctuating inland wetlands were dominated by species that fail to resprout after a dry-down cycle, and fewer species occupied the persistence niche (33%) than the regeneration niche. At the local scale, the proportion of resprouting species also varied with degree of disturbance, with higher occupancy of the persistence niche (clonal resprouters) in the more stable environments (deep basins) of these wetlands over time (table 4). These patterns of resprouting traits support the model of Bellingham and Sparrow (2000), where at very high disturbance frequencies, the number of resprouting species declines and systems become dominated by therophytes or short-lived species, as shown in the predicted decline of resprouting to the right in figure 1. Whether this shift in occupancy of the persistence niche in wetlands is a global phenomenon or restricted to Australia because of its climate 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 resprouting. Subsequently, new ramets quickly develop roots and shoots for growth and storage. Our field-based observations suggest that clonality of perennial wetland species is a good surrogate for attributing resprouting after dry-down and possibly other disturbances (grazing and fire). The size of the clonal storage organs will, however, influence resprouting ability, as will species interactions (competition and herbivory; Klimošová and Klimeš 2007) and disturbance frequency (this study). This differs from terrestrial systems dominated by perennial woody resprouters, where the proportion of resprouting species that are clonal is relatively small (Clarke et al. 2010). Even within the terrestrial herbaceous floras, the proportion of resprouting species that are clonal does not approach the levels of clonality found in the more stable wetland systems (Abrahamson 1980; Kautsky 1988; Barrett et al. 1993; Grace 1993; Klimeš et al. 1997).

Trait Trade-offs in Disturbance Tolerance

We argue that the ability to maintain and to protect a bud bank and to store carbohydrates for resprouting in clonal and other resprouting species is constrained by frequency of disturbance (dry downs). This idea is supported by studies that show that resprouters (clonal species) with low reproductive output are more likely to occur in stable wetlands,

whereas ruderals are associated with more disturbance-prone habitats (fluctuating water levels; Willby et al. 2000; Deil 2005). The size of bud banks has also been recently shown to correlate with disturbance, with small bud banks associated with disturbed habitats (Klimošová and Klimeš 2007). Furthermore, there is evidence of trade-offs with sexual reproduction in wetland plants, where clonal species allocate fewer resources to reproduction (Dorken et al. 2004). While short-lived or semelparous species fill much of the regeneration niche, we also found nonsprouting perennial species present under high-disturbance frequencies (table 2). Unexpectedly, most species occupying the regeneration niche were not neophytes but cosmopolitan. Such high levels of nonsprouters align with other frequently disturbed habitats such as vernal pools, ephemeral rock pools, ephemeral flush vegetation, and cultivated fields where ruderal life histories are predicted to occur (e.g., Zedler 2003; Crawley 2004; Deil 2005; Rhazi et al. 2009). More generally, our results are consistent with the well-known habitat templet model, in which disturbed habitats are dominated by generalists at the *r* end of the *r*-*K* spectrum (Grime 1977; Southwood 1977).

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/congener 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-

tween 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 (Kneitel 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 trait trade-offs such as competitive ability and predator tolerance influence community assembly.

Acknowledgments

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