EVALUATING A STRATEGY TO ENHANCE BIODIVERSITY OVER A 426-HA PRAIRIE RESTORATION AFTER 10 YEARS

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Abstract

Restoring high levels of biological diversity in landscape restoration work is critical to reestablishing many important ecological functions. In large restorations, this often presents a significant challenge in that seed acquisition is often limited by either financial resources or availability, or both, especially for rare species or those producing little seed. To increase diversity across 426 ha of wet to dry prairie in a 1,113 ha restoration in northern Illinois, 89 species were planted in 60 30-m diameter 'nodes of diversity' to enhance a base seeding of 61 matrix species through ongoing dispersal. Twenty eight nodes were planted with 54 wet prairie species (wet species), 26 nodes with 48 mesic prairie species (mesic species), and six nodes with 33 dry prairie species (dry species). Dispersal potential of node species ranged from low (e.g. gravity dispersal) to high (e.g. wind or animal-vector dispersal). After 10 growing seasons, each node was assessed for species establishment and abundance, with occurrence and abundance assessed in consecutive rings outside each node at 5-m increments to determine if dispersal from nodes was a viable means of increasing diversity across the restoration site.

Eighty node species established in at least one node, with 94.0 % of wet, 79.2 % of mesic, and 87.9 % of dry species found. Nodes averaged 13.7 species in wet prairie, 12.8 species in mesic prairie, and 17.3 species in dry prairie. Not all established species successfully dispersed: 43 % of wet, 45% of mesic, and 46 % of dry species established in the first 5-m ring outside the nodes; 23 % of wet species, 27 % of mesic species, and 30 % of dry species established in the second ring, and 8% of wet species, 8 % of mesic species, and 28 % of dry species established in the third ring.

Establishment potential following dispersal was unrelated to dispersal potential, as no differences were found among the three dispersal potential classes in the proportion of established species that dispersed within any of the three habitat type. However, based on casual monitoring, species with higher dispersal potential did establish well beyond the 60-m diameter area surveyed at each node, but at densities too low to effectively sample, or to make diversity nodes a viable strategy to increase diversity *evenly* across the site over a 10-year period. However, the nodes were successful in introducing species where little seed was affordable or available in densities that promoted the establishment and expansion of viable populations. These nodes now serve as a focus for seed collection for ongoing introductions elsewhere.

Introduction

A general consensus has developed that a positive relationship exists between biological diversity and ecological function (Hooper and Vitousek 1997, Zedler et al. 2001, Cardinale 2002, Lambers et al. 2004, Hooper et al. 2005, Balvanera et al. 2006, Tilman et al. 2006, Hillebrand and Matthiessen 2009, Quijas et al. 2010, Hector et al. 2011, Morin et al. 2011, Midgley 2012, Quijas et al. 2012, Turnbull et al. 2012). From a conservation perspective, particularly in regard to the restoration of globally rare landscapes such as tallgrass prairie, restoring high levels of biological diversity is critical to establishing and maintaining ecological function (Schwartz et al. 2000, Callaway 2003, Naeem 2006, Duffy 2009, Webster et al. 2010, Biondini et al. 2011, Isbell et al. 2011, Symstad and Jonas 2011, Tilman et al. 2012, Isbell et al. 2013). One of the most difficult challenges restoring plant species diversity in large-scale restoration is securing a sufficient quantity of native plant propagules for each species targeted for reintroduction. Many species that once characterized native landscapes may not be available as they are locally extirpated or rare, and/or they produce very little seed (Howe 1994, Polley et al. 2005). Many species that are not particularly rare within their native habitat may still be difficult or expensive to acquire if little of their habitat remains (Packard 1997). In large restorations, seed acquisition is often limited by both financial resources and availability, especially of rare species or those producing little seed (Rowe 2010, Larson et al. 2011).

To increase prairie species diversity across 426 ha being restored as wet-, mesic-, and dry prairie, we planted 60 730 m^2 diversity 'nodes' to enhance the matrix of species planted in each of the three prairie habitats through species dispersal over a 10 year period. Our goal was to determine:

1) Can the introduction of species in diversity nodes be used as an effective strategy to increase species diversity outside the nodes through ongoing dispersal across a restoration site?
2) Are species with higher dispersal potential better at establishing beyond the diversity nodes?
3) Are some species better than others at both establishing in nodes and dispersing across the site?

Methods

In 2001, restoration efforts began on 1,113 ha of land that had been planted in corn and soybeans since 1909 to a landscape mosaic of lakes, wetlands, savanna, forest, and prairie (the Sue and Wes Dixon Waterfowl Refuge at Hennepin & Hopper Lakes, now a RAMSAR wetland of international importance). Because of finite financial resources and the inherent scarcity of some species, one of the primary challenges was to acquire sufficient seed to establish high levels of plant diversity on the 426 ha being restored. A matrix of 61 species was planted across the three types of prairie, with each type identified on the landscape based on topography, soil characteristics, and predicted hydrology. Species were introduced from seed through 'frost seeding', i.e., seed was planted in late autumn once nights were cold enough to produce frost-heaving, which combined with daytime melting naturally worked seed into exposed mineral soil.

As a strategy to enhance prairie species diversity, 60 30-m diameter 'nodes' of diversity (each 730 m^2; Figure 1) were planted with 89 additional species: 28 nodes with 50 wet prairie species (wet species), 26 nodes with 48 mesic prairie species (mesic species), and six nodes with 33 dry prairie species (dry species). The number of nodes was proportional to the area of each type of prairie planted. Nodes were located across the landscape objectively to insure that at least one node was found in each contiguous section of prairie habitat, i.e., each discrete habitat unit had at least one node from which node species could potentially disperse (Figure 2). Consequently, node density was related to the spatial distribution of all habitats across the landscape mosaic. Each node was marked with a steel stake and the coordinates recorded with GPS. The quantity of seed per species varied among species in each node based on cost and availability (Table 1), but in all cases was much less than that of the matrix species planted.

The dispersal potential of each node species was subjectively assigned to one of three dispersal classes based on their physical characteristics. Species ranged from low potential (e.g. gravity dispersal with the heavy round seeds of *Baptisia leucantha*) to high potential (e.g. wind dispersal aided by the fluffy pappus on seeds of *Asclepias tuberosa*, or animal-vector dispersal with the sticky seeds of *Desmodium illinoense*). Some species were categorized as intermediate due to seed characteristics that appear to promote longer dispersal under specific conditions, e.g. the fine seeds of *Penstemon digitalis* which are shaken from capsules in wind. After 10 growing seasons, each node was assessed for species establishment and abundance, with abundance assessed in consecutive rings outside each node at 5-m increments to determine if dispersal from nodes was a viable means of increasing diversity evenly across the restoration site. Of the 60 nodes planted in 2002, 53 were sampled in 2012: 26 wet, 23 mesic, and four dry (seven were lost, e.g. one suffering an invasion of Canada thistle was eradicated). Differences among species with different dispersal potentials were assessed with a non-parametric Kruskal-Wallis test, with post hoc Bonferroni pairwise comparisons calculated to assess differences among percent-depletion means.

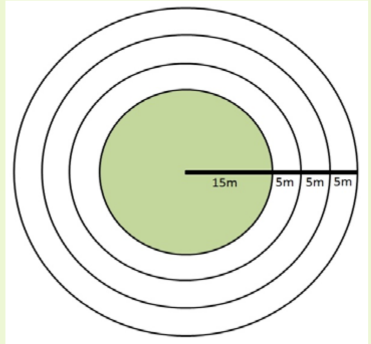


Figure 1. Layout of 730 m^2 diversity nodes planted in 2002 (15-m diameter circle, in green), with consecutive rings at 5 m intervals that were sampled to record dispersal outside each node (rings at 15 to 20-, 20 to 25-, and 25 to 30 m from center).

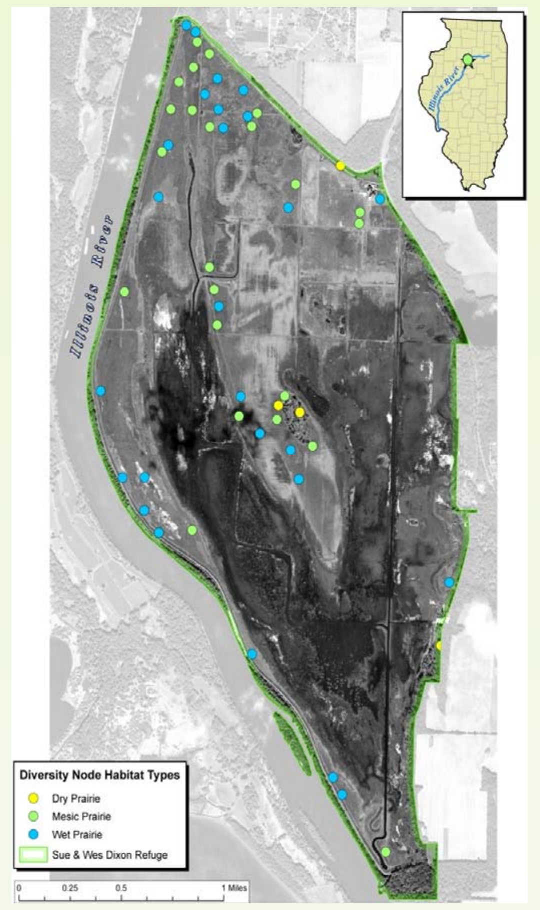


Figure 2. Distribution of 53 30-m diameter diversity nodes surveyed in 426 ha of wet-, mesic-, and dry prairie in 2002 at the 1,113-ha Sue and Wes Dixon Waterfowl Refuge at Hennepin & Hopper Lakes.

Table 1. Identity and quantity of seed for each species planted in a wet-, mesic, or dry prairie diversity node. Note that some species appear in more than one habitat due to naturally overlapping distributions.

	wet species	seed / node	mesic species	seed / node	dry species	seed / node
1	Agalinus purpurea	10,714	Allium cernuum	3,691	Allium stellatum	12,857
2	Allium cernuum	3,257	Asclepias sullivantii	83	Antennaria plantaginifolia	8,100
3	Asclepias incarnata	86	Baptisia leucantha	911	Asclepias hirtella	934
4	Asclepias sullivantii	115	Baptisia leucophaea	120	Asclepias tuberosa	1,229
5	Aster praealtus	1,021	Bouteloua curtipendula	5,357	Aster sericeus	2,000
6	Baptisia leucantha	911	Bromus kalmii	9,821	Astragalus canadensis	4,571
7	Bidens aristosa	321	Carex bicknellii	300	Bouteloua curtipendula	16,071
8	Bidens coronata	446	Cassia marilandica	971	Bromus kalmii	19,643
9	Boltonia asteroides	25,313	Coreopsis tripteris	1,250	Carex bicknellii	651
10	Cacalia plantaginea	54	Dalea candida	10,179	Carex muhlenbergii	493
11	Carex buxbaumii	189	Dalea purpurea	2,571	Coreopsis lanceolata	5,714
12	Cicuta maculata	321	Desmanthus illinoensis	750	Coreopsis palmata	3,571
13	Coreopsis tripteris	1,250	Desmodium canadense	381	Coreopsis tripteris	2,250
14	Desmanthus illinoensis	750	Desmodium Illinoense	768	Dalea candida	20,527
15	Desmodium canadense	454	Dodecatheon meadia	1,071	Desmanthus illinoensis	1,500
16	Eleocharis erythropoda	583	Echinacea pallida	3,714	Desmodium canadense	1,571
17	Eleocharis obtusa	357	Euphorbia corollata	429	Desmodium illinoensis	176
18	Gentiana andrewsii	2,690	Gentiana andrewsii	2,640	Echinacea pallida	7,429
19	Helenium autumale	4,643	Gentiana flavida	5,000	Euphorbia corollata	800
20	Hypericum pyramidatum	33,750	Gentiana puberulenta	6,214	Helianthus rigidus	411
21	Iris virginicus	89	Helianthus rigidus	205	Hypericum sphaerocarpon	6,714
22	Juncus dudleyi	8,929	Heuchera richardsonii	2,500	Koeleria cristata	10,045
23	Juncus effusus	35,714	Hypericum pyramidatum	33,750	Lespedeza capitata	1,429
24	Juncus torreyi	2,857	Hypericum sphaerocarpon	3,357	Liatris aspera	17,143
25	Liatris pycnostachya	1,286	Koeleria cristata	5,022	Monarda punctata	12,857
26	Lobelia spicata	1,527	Liatris aspera	10,000	Panicum leibergii	357
27	Lycopus americanus	3,872	Liatris pycnostachya	1,286	Parthenium integrifolium	625
28	Lycopus uniflorus	30,179	Parthenium integrifolium	750	Penstemon digitalis	83,571
29	Lysimachia quadriflora	4,259	Pedicularis canadensis	943	Penstemon pallidus	6,429
30	Lythrum alatum	18,214	Physostegia virginiana	209	Potentilla arguta	23,821
31	Mentha arvensis	10,714	Potentilla arguta	12,321	Rosa carolina	134
32	Mimulus ringens	44,768	Pycnanthemum pilosum	3,304	Solidago nemoralis	10,714
33	Parthenium integrifolium	500	Pycnanthemum virginianum	92,714	Tradescantia ohiensis	3,143
34	Physostegia virginiana	273	Rosa carolina	134		
35	Pycnanthemum virginianum	91,143	Silphium integrifolium	386		
36	Rosa carolina	134	Silphium perfoliatum	150		
37	Rudbeckia fulgida sullivantii	3,654	Silphium laciniatum	1,850		
38	Rudbeckia triloba	5,009	Silphium terebinthinaceum	1,000		
39	Scirpus atrovirens	348,286	Sisyrinchium albidum	1,367		
40	Scirpus pendulus	8,957	Solidago graminifolia	2,500		
41	Scirpus validus	1,107	Solidago juncea	7,857		
42	Senecio pauperculus	1,250	Solidago nemoralis	5,357		
43	Silphium integrifolium	386	Solidago riddellii	9,964		
44	Silphium laciniatum	1,084	Solidago speciosa	1,357		
45	Silphium perfoliatum	150	Tradescantia ohiensis	857		
46	Silphium terebinthinaceum	1,000	Vernonia fasciculata	4,371		
47	Solidago graminifolia	2,500	Veronicastrum virginicum	57,286		
48	Solidago riddellii	9,964	Zizea aurea	1,768		
49	Teucrium canadense	6,429				
50	Thalictrum dasycarpum	1,964				
51	Tradescantia ohiensis	714				
52	Vernonia fasciculata	5,229				
53	Veronicastrum virginicum	57,286				
54	Zizea aurea	1,768				

Results and Discussion

Eighty node species established in at least one node, with 94.0 % of wet, 79.6 % of mesic, and 78.4 % of dry species found. Nodes averaged 13.7 species in wet prairie, 12.8 species in mesic prairie, and 17.3 species in dry prairie. Not all species that established successfully within each node dispersed (Table 2). Fewer numbers of species dispersed into each consecutive ring surveyed outside the nodes, and most species were not found more than 15 m beyond the outer edge of the nodes, indicating that most dispersal after 10 years was relatively short distance. There was a notable exception in the wet prairie habitat where two species (*Desmanthus illinoense* and *Bidens aristosa*) established in high densities within the footprint of a few surface drainage ways that resulted in longer term moist soil conditions. These species have colonized large portions of the site where those specific conditions have been found. One unexpected outcome was the greater number of species established in dry prairie nodes and the greater proportion of dry prairie species that dispersed into each consecutive ring surveyed despite the generally low recruitment observed in dry prairie in moderate to dry years.

Table 2. The mean proportion of established species that dispersed to each consecutive ring surveyed outside the nodes within each habitat.

habitat	15-20m	20-25m	25-30m
wet	0.430	0.225	0.078
mesic	0.449	0.270	0.081
dry	0.457	0.301	0.278

Some species did not establish anywhere and others that did establish failed to disperse outside the nodes, while some species were quite good at recruitment as more individuals were found outside the nodes than within (Table 3). Some of these species are relatively conservative and most likely encountered in less-disturbed communities, such as *Liatris pycnostachya* or *Echinacea pallida*, indicating that at least some conservative species can be introduced at lower densities and still populate a restoration. This appears to have happened more consistently around wet habitat nodes, perhaps where soil moisture was less of a constraint to recruitment than in the drier areas. This further suggests a subset of species that could be planted from seed in lower densities, while other species that might be better introduced as plugs.

Wet prairie node

Mesic prairie node

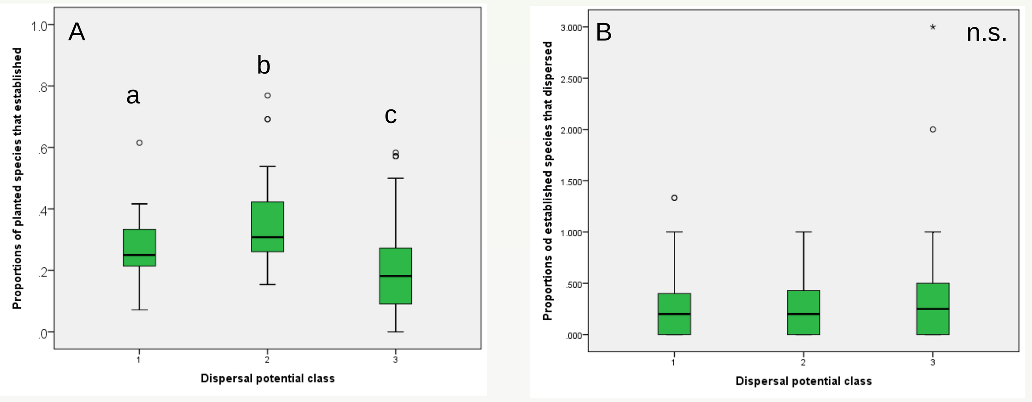
Dry prairie node being surveyed

Table 3. Mean ratio of dispersed to established individuals (D = number dispersed outside the node / number established within the node) for each wet-, mesic-, and dry prairie species. No value indicates that no individuals established, while 0.000 means that no individuals dispersed outside the node.

	wet species	D	mesic species	D	dry species	D
1	Juncus effusus	4.868	Desmodium canadense	8.603	Penstemon digitalis	1.820
2	Solidago graminifolia	4.000	Liatris pycnostachya	1.208	Bouteloua curtipendula	1.364
3	Liatris pycnostachya	2.269	Desmanthus illinoensis	0.942	Desmodium illinoensis	1.071
4	Silphium perfoliatum	1.776	Vernonia fasciculata	0.882	Echinacea pallida	1.021
5	Silphium integrifolium	1.387	Desmodium Illinoense	0.820	Carex muhlenbergii	0.917
6	Desmanthus illinoensis	1.329	Coreopsis tripteris	0.669	Monarda punctata	0.833
7	Bidens aristosa	1.243	Asclepias sullivantii	0.647	Koeleria cristata	0.617
8	Mentha arvensis	0.833	Dalea purpurea	0.630	Penstemon pallidus	0.563
9	Lycopus americanus	0.798	Solidago nemoralis	0.623	Coreopsis lanceolata	0.561
10	Scirpus pendulus	0.595	Zizea aurea	0.583	Lespedeza capitata	0.442
11	Scirpus validus	0.577	Echinacea pallida	0.361	Coreopsis palmata	0.321
12	Silphium terebinthinaceum	0.506	Bromus kalmii	0.333	Desmodium canadense	0.188
13	Silphium laciniatum	0.302	Veronicastrum virginicum	0.288	Coreopsis tripteris	0.167
14	Physostegia virginiana	0.256	Silphium perfoliatum	0.229	Parthenium integrifolium	0.167
15	Asclepias incarnata	0.235	Parthenium integrifolium	0.217	Asclepias tuberosa	0.143
16	Zizea aurea	0.223	Hypericum pyramidatum	0.167	Allium stellatum	0.091
17	Cicuta maculata	0.212	Silphium laciniatum	0.147	Potentilla arguta	0.042
18	Eleocharis erythropoda	0.188	Koeleria cristata	0.127	Solidago nemoralis	0.014
19	Vernonia fasciculata	0.160	Silphium terebinthinaceum	0.103	Dalea candidum	0.012
20	Helenium autumale	0.152	Baptisia leucantha	0.093	Antennaria plantaginifolia	0.000
21	Lythrum alatum	0.125	Pycnanthemum virginianum	0.083	Asclepias hirtella	0.000
22	Tradescantia ohiensis	0.125	Solidago speciosa	0.069	Aster sericeus	0.000
23	Boltonia asteroides	0.114	Silphium integrifolium	0.067	Astragalus canadensis	0.000
24	Coreopsis tripteris	0.108	Tradescantia ohiensis	0.063	Carex bicknellii	0.000
25	Scirpus atrovirens	0.103	Bouteloua curtipendula	0.057	Euphorbia corollata	0.000
26	Baptisia leucantha	0.077	Pycnanthemum pilosum	0.056	Helianthus rigidus	0.000
27	Pycnanthemum virginianum	0.070	Carex bicknellii	0.050	Liatris aspera	0.000
28	Veronicastrum virginicum	0.045	Baptisia leucophaea	0.009	Rosa carolina	0.000
29	Mimulus ringens	0.042	Dalea candidum	0.000	Tradescantia ohiensis	0.000
30	Juncus torreyi	0.010	Euphorbia corollata	0.000	Bromus kalmii	
31	Agalinus purpurea	0.000	Gentiana flavida	0.000	Desmanthus illinoensis	
32	Allium cernuum	0.000	Gentiana puberulenta	0.000	Hypericum sphaerocarpon	
33	Asclepias sullivantii	0.000	Hypericum sphaerocarpon	0.000	Panicum leibergii	
34	Cacalia plantaginea	0.000	Physostegia virginiana	0.000		
35	Carex buxbaumii	0.000	Rosa carolina	0.000		
36	Desmodium canadense	0.000	Solidago graminifolia	0.000		
37	Gentiana andrewsii	0.000	Solidago juncea	0.000		
38	Hypericum pyramidatum	0.000	Allium cernuum			
39	Iris virginicus	0.000	Cassia marilandica			
40	Juncus dudleyi	0.000	Dodecatheon meadia			
41	Lobelia spicata	0.000	Gentiana andrewsii			
42	Lysimachia quadriflora	0.000	Helianthus rigidus			
43	Parthenium integrifolium	0.000	Heuchera richardsonii			
44	Rosa carolina	0.000	Liatris aspera			
45	Solidago riddellii	0.000	Pedicularis canadensis			
46	Teucrium canadense	0.000	Potentilla arguta			
47	Thalictrum dasycarpum	0.000	Sisyrinchium albidum			
48	Aster praealtus		Solidago riddellii			
49	Bidens coronata					
50	Eleocharis obtusa					
51	Lycopus uniflorus					
52	Rudbeckia fulgida					
53	Rudbeckia triloba					
54	Senecio pauperculus					

There were significant differences among the three dispersal potential classes in the proportion of species planted that established across all habitat types (Figure 3). A significantly smaller proportion of species established that were ranked in the highest dispersal potential class, with the greatest proportion of species establishing within the nodes from the group ranked as intermediate in dispersal potential (intermediate > low > high). However, there were no differences among the three dispersal potential classes in the proportion of species that dispersed outside the nodes, suggesting that dispersal potential (as defined in this experiment) is not a good predictor of successful establishment following dispersal. Since successful dispersal (establishment following dispersal) was not related to dispersal mechanism, the choice of species for introduction at lower densities (to disperse and increase from recruitment) should be independent of dispersal mechanism and how they interact with a given site.

Figure 3. Box plot of the proportion of each species planted that established from each dispersal potential class across all habitat types (A), with a box plot of the proportion of species planted that dispersed outside the nodes among the three dispersal potential classes (B). Overall differences among means assessed with a Kruskal-Wallis analysis, with differences among means assessed with post hoc Bonferroni pairwise comparisons.



No differences were found among the three dispersal potential classes in the proportion of established species that dispersed within any of the three habitat types (Table 4, Figure 4). Although the mean proportion of species that dispersed from each dispersal potential class differed among nodes, success varied widely among nodes and appeared to be strongly influenced by local conditions unrelated to species or group identity. Not all wet prairie nodes were equally wet, nor dry prairie nodes equally dry. Soil characteristics varied among nodes as well (e.g. sandy vs. clayey), leading to differences in the conditions influencing successful establishment. Likely of equal importance was local community dynamics, which varied widely in both invasive pressure, and the relative densities of and among established species. This again suggests that dispersal mechanism is not a good predictor of successful establishment following dispersal locally, despite some species having a greater potential for long distance dispersal.

Figure 4. Box plots of the mean proportion of established species in each node that dispersed outside the node among the three dispersal potential classes in each habitat. In each case, differences among dispersal classes were not significant (Kruskal-Wallis).

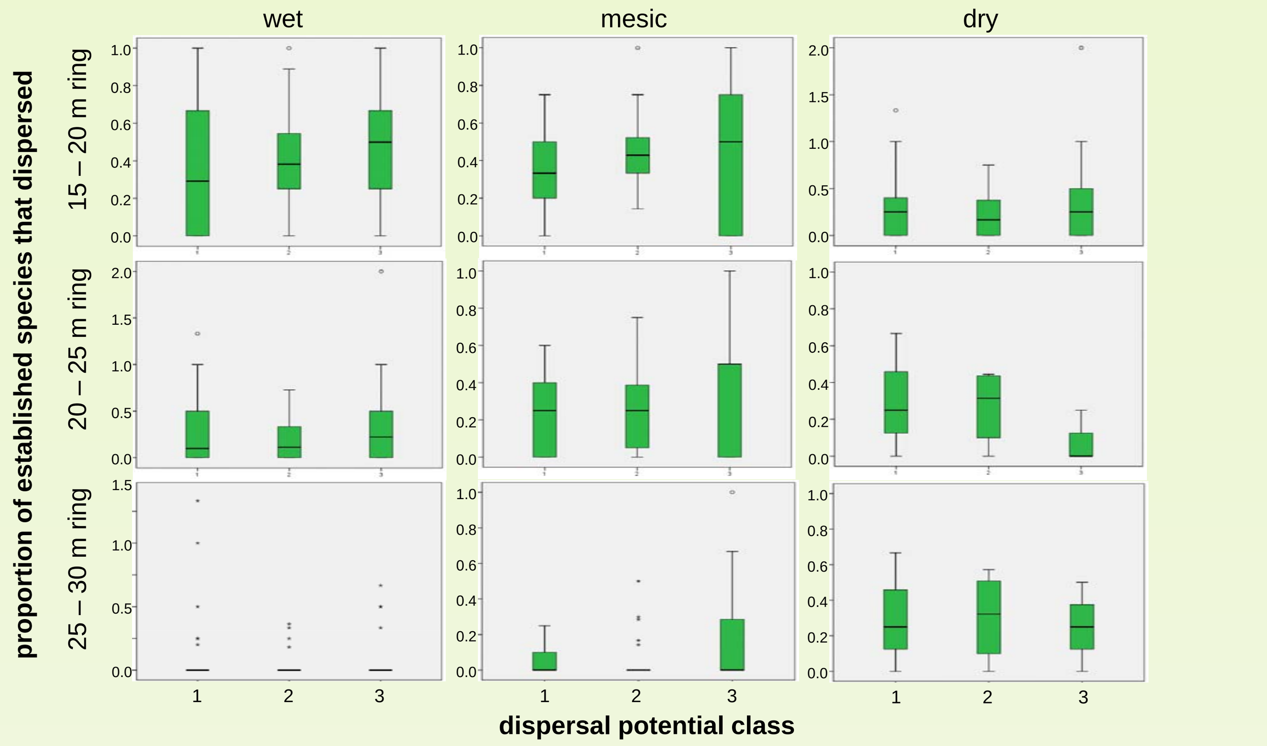


Table 4. The mean proportion of established species of each dispersal type that dispersed to each consecutive ring surveyed outside the nodes within each habitat. Differences among dispersal types for each habitat type at each consecutive ring were not significant (Kruskal-Wallis).

dispersal ring	habitat	dispersal type		
		1	2	3
	wet	0.387	0.384	0.574
15-20 m	mesic	0.323	0.466	0.479
	dry	0.454	0.526	0.250
	wet	0.280	0.174	0.356
20-25 m	mesic	0.228	0.250	0.375
	dry	0.342	0.324	0.188
	wet	0.126	0.050	0.091
25-30 m	mesic	0.046	0.053	0.158
	dry	0.292	0.304	0.188

Conclusions

Dispersal from diversity nodes was not a viable strategy to increase species diversity evenly across the 426-ha site over a 10-year period. However, the nodes were successful in introducing species locally where little seed was affordable or available, and these nodes now serve as a focus for seed collection efforts to support ongoing introductions elsewhere. Furthermore, some species did disperse outside the node to begin 'mini' single-species nodes of dispersal, but at densities too low to effectively sample, or to determine origin. Although many species can and will disperse effectively, 10 years is too short a period for this strategy to effectively increase plant diversity evenly across a large restoration site.

In general, species with higher dispersal potential were slightly less better at dispersing effectively within the local area outside the nodes, indicating that dispersal potential is not a reliable predictor of establishment success. Establishment success following dispersal is more likely a function of both seed provisioning and the local physical, chemical, and biological characteristics of the site. However, some species, independent of dispersal characteristics, were clearly better at successful establishment following dispersal than others. Where seed quantities are limited, these species would be good candidates for planting from seed at lower densities to naturally populate a site through successful recruitment. Those species that are poor at establishing as well as dispersal would be better introduced as greenhouse grown plugs, especially where little seed is available or affordable.

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