



Coexistence of *Typha latifolia*, *T. angustifolia* (Typhaceae) and their invasive hybrid is not explained by niche partitioning across water depths



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ABSTRACT

Spatial separation between hybridizing taxa can limit hybridization and introgression when mating occurs between near neighbours. Water depth can be an important factor structuring wetland plant communities, which often include cattails (*Typha* spp., Typhaceae). In eastern North America, native *Typha latifolia* regularly hybridizes with introduced *T. angustifolia* to produce the invasive F₁ hybrid *T. × glauca*, which can backcross to parental species. Hybridization in this wind-pollinated species complex may be facilitated by overlapping niches among taxa, but previous studies have yielded contradictory results, possibly because these studies were limited to shallow sites or single locations. We investigated patterns of depth occupancy in ditches (mean depth 3.4 cm) and permanent wetlands (mean depth 25.0 cm) with various mixtures of *T. latifolia*, *T. angustifolia*, and *T. × glauca* across a 1700 km transect from Michigan, USA, to Nova Scotia, Canada. Overall, we found that water depth cannot on its own explain patterns of cattail occupancy. We therefore conclude that niche partitioning by water depth does not promote mating isolation in *Typha*. Previous findings of habitat segregation by depth may be attributable to a combination of idiosyncratic features of individual sites, multi-dimensional niches, and phenotypic plasticity, which could prevent consistent niche segregation among *Typha* taxa. A lack of spatial segregation between *Typha* taxa should promote hybridization and introgression. This, coupled with the competitive superiority of hybrids, appears to be facilitating the displacement of native *T. latifolia* across a wide geographical range.

1. Introduction

Biological invasions and habitat modification are primary threats to native species diversity (Butchart et al., 2010). These threats can be compounded when introduced species hybridize with native flora and fauna (Todesco et al., 2016). In such cases, mechanisms that prevent hybrid formation and/or persistence play a central role in the maintenance of native species diversity. For plants, differences in habitats between potentially hybridizing species are an important reproductive barrier ('ecogeographic isolation'; Sobel et al., 2010) because mating tends to occur between near-neighbours (Levin and Kerster 1974) rendering habitat segregation, and therefore spatial segregation between heterospecifics, an effective means of limiting hybridization. For example, two species of watermilfoil, *Myriophyllum spicatum* and *M. sibiricum*, whose hybrid is invasive in North America (Moody and Les, 2002) exhibit limited hybridization in regions where there is little overlap in climatic niches between parent species (Wu et al., 2015). Habitat segregation between taxa can remain important for native biodiversity even if viable hybrids are formed, as habitat segregation

between hybrids and progenitors can impact the frequency and direction of genetic introgression between species. Additionally, where habitat segregation among parent species and their hybrid is lacking, native plants may be at greater risk of competitive displacement from hybrids than from a non-native progenitor alone (e.g. *Spartina foliosa*, Ayres et al., 2004).

Water depth can strongly influence the structuring of aquatic plant communities, both directly and indirectly (Sculthope, 1967; Lacoul and Freedman, 2006). Water depth can act directly on community structuring by driving niche segregation among even closely related species (e.g. *Spartina densiflora* and *S. maritima*, Castillo et al., 2010; *Ceratophyllum demersum* and *C. submersum*, Nagengast and Gabka, 2017). Indirect effects of water depth can be mediated by competitive interactions in which water depth and the presence of neighbouring species interact to drive niche segregation (Boschilia et al., 2008). For example, in the absence of its congeneric *Spartina maritima*, *S. densiflora* can occupy a wide range of intertidal elevations (Castillo et al., 2000). However, *S. densiflora* occupies only mid- to high elevations when growing with *S. maritima* despite appropriate physiochemical

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Table 1Location and site characteristics of *Typha* stands sampled during June and July 2013. Numbers and percentages of each taxon in a site are based on ramets.

Location	Site Type	Site code	Location (°N, °W)	Distance between sites at location (km)	# (%) <i>T. angustifolia</i>	# (%) <i>T. latifolia</i>	# (%) <i>T. × glauca</i>	Composition type
Cheboygan, MI	Ditch	CHD	45.641, 84.459	2.10	15 (16)	0 (0)	77 (84)	Two-taxa
	Wetland	CHW	45.645, 84.424		45 (47)	0 (0)	51 (53)	Two-taxa
Lapeer, MI	Ditch	LAD	43.043, 83.328	3.95	29 (33)	24 (28)	34 (39)	Three-taxa
	Wetland	LAW	43.018, 83.361		15 (16)	13 (13)	68 (71)	Three-taxa
West Branch, MI	Ditch	WBD	44.276, 84.269	14.20	10 (12)	0 (0)	76 (88)	Two-taxa
	Wetland	WBW	44.404, 84.268		0 (0)	47 (48)	51 (52)	Two-taxa
Pickering, ON	Ditch	PID	43.834, 79.060	2.11	0 (0)	0 (0)	75 (100)	Single-taxon
	Wetland	PIW	43.820, 79.042		51 (64)	5 (6)	24 (30)	Three-taxa
Kingston, ON	Ditch	ODD	44.250, 76.572	3.48*	0 (0)	47 (48)	49 (51)	Two-taxa
	Wetland	ODW	44.252, 76.616*		0 (0)	1 (1)	83 (99)	Two-taxon
Cornwall, ON	Ditch	COD	45.044, 74.750	6.57	28 (29)	38 (40)	29 (31)	Three-taxa
	Wetland	COW	45.042, 74.833		0 (0)	5 (6)	83 (94)	Two-taxa
Montmagny, QC	Ditch	MOD	46.937, 70.653	132.31	4 (6)	40 (60)	23 (34)	Three-taxa
	Wetland	MOW	47.726, 69.340		0 (0)	96 (100)	0 (0)	Single-taxon
Edmundston, NB	Ditch	EDD	47.034, 67.768	18.18	0 (0)	62 (93)	5 (7)	Two-taxa
	Wetland	EDW	47.159, 67.922		0 (0)	66 (80)	16 (20)	Two-taxa
Fredericton, NB	Ditch	FRD	45.924, 66.634	7.95	0 (0)	65 (96)	3 (4)	Two-taxa
	Wetland	FRW	45.887, 66.634		0 (0)	105 (100)	0 (0)	Single-taxon
Sackville, NS	Ditch	SAD	45.870, 64.132	14.66	1 (2)	9 (14)	52 (84)	Three-taxa
	Wetland	SAW	45.973, 64.016		0 (0)	79 (100)	0 (0)	Single-taxon
Halifax, NS	Ditch	HAD	44.739, 63.253	16.86	1 (2)	65 (98)	0 (0)	Two-taxa
	Wetland	HAW	44.705, 63.460		0 (0)	69 (95)	4 (5)	Two-taxa

* Precise location of site and distance between sites estimated.

conditions for the former's growth at lower elevations, suggesting that it is being competitively excluded from lower elevations by *S. maritima* (Castillo et al., 2008).

Cattails (*Typha* spp., Typhaceae) are a common emergent plant of wetland habitats around the world. In northeastern North America, three cattail taxa occur: the native *T. latifolia* L., (broad-leaved cattail); *T. angustifolia* L., (narrow-leaved cattail), which was introduced from Europe several centuries ago (Ciotir et al., 2013a; Ciotir and Freeland, 2016); and their F₁ hybrid *T. × glauca* Godr., (Smith, 1967). *Typha × glauca* is particularly common in the Midwestern USA (Travis et al., 2010) and southern Ontario and Quebec, Canada (Kirk et al., 2011; Freeland et al., 2013) where it appears to have a competitive advantage over its parental species (Bunbury-Blanchette et al., 2015; Zapfe and Freeland, 2015). It has been described as highly invasive in parts of its range (Galatowitsch et al., 1999) and threatens to displace native *T. latifolia* in the Laurentian Great Lakes region (Pieper et al., 2017). Although studies from a small number of sites have reported niche segregation by water depth among cattail taxa (Grace and Wetzel, 1981a, 1998; Travis et al., 2010), evidence in support of niche segregation is mixed. Travis et al. (2010) found that *T. latifolia* occupied shallower depths than both *T. × glauca* and *T. angustifolia* in a mixed population though they were unable to determine whether taxa were restricted to particular water depths in single-species stands. A larger sampling of sites in south-eastern Ontario found no evidence that *Typha* taxa segregate along elevational gradients within sites (McKenzie-Gopsill et al., 2012). However, that study included a large proportion of sites that occurred in ditches, which are likely to have a narrower range of water depths compared to open marsh habitats, potentially reducing the scope for detecting niche segregation (and see Zapfe and Freeland, 2015). Cattail species are difficult to distinguish morphologically in areas where introgression occurs, making practical management options to reduce hybrid prevalence very challenging. Management therefore requires a greater understanding of ecological characteristics, such as habitat occupancy of taxa, that could influence the pervasiveness of hybrids.

Here we present an examination of water depths occupied by different cattail taxa across a broad spatial scale to test the notion that northeastern North American cattails are subject to habitat segregation by water depth, and to understand why results have been mixed on this topic. As previous reports of water depth segregation in *Typha* have

been based on distributions within single sites (Grace and Wetzel, 1981a, 1998; Travis et al., 2010), we sampled 22 *Typha* stands to determine whether patterns of depth occupancy by taxa are consistent. Furthermore, we tested whether patterns of segregation by water depth among cattails depended on whether they were growing in large, open wetlands or in ditch habitats since, as noted above, a previous test of the hypothesis might have been biased because of the inclusion of ditch sites in the analysis (McKenzie-Gopsill et al., 2012). Whenever possible we attempted to sample sites in which at least two taxa were growing, but the frequencies of the different species vary across regions, with high frequencies of *T. angustifolia* and hybrid cattails in the Midwestern USA and high frequencies of *T. latifolia* in eastern Canada (Travis et al., 2010; Freeland et al., 2013). For this reason, our sampled sites included a mix of taxonomic compositions, ranging from single-taxon sites for *T. latifolia* and *T. × glauca* to sites where all three taxa were present. Using this mixture of habitats and taxonomic compositions we asked: (1) Is there evidence that different cattail taxa occupy different water depths? (2) If so, do patterns of segregation by water depth depend on the range of water depths at a site (i.e. do patterns depend on whether cattails were growing in large, open and relatively deep marshes, or in relatively shallow ditch habitats?); and (3) Do stands with different taxonomic compositions differ in their patterns of water-depth segregation? For the latter question we were particularly interested in whether the presence of hybrid cattails affected the distribution of water depths occupied by native *T. latifolia*. Because previous findings of differences in water depth-occupancy patterns have come from single sites (Grace and Wetzel, 1981a; Travis et al., 2010), we further asked (4) whether patterns of water depth occupancy differ between individual sites. A positive answer to this last question would indicate that patterns of water depth occupation depend on additional factors not considered here or in previous studies and may therefore reflect idiosyncratic features of individual wetlands (e.g. the history of colonization of the wetland by each species) instead of overall differences in water-depth occupation among taxa.

2. Methods

2.1. Sampling and depth measurements

In June and July 2013 we sampled cattails growing in paired

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