MEASURING DOMINANCE AMONG CO-OCCURRING PLANTS

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Introduction

Great Lakes coastal wetlands respond to constantly changing environments and water levels with a dynamic, ever changing plant community (van der Valk 1981). In such wetlands, the proportions and sizes of communities are expected to change from year to year, along with species composition. When impacts of climate change and invasive species are added to natural variations, one can anticipate further changes in the species that are dominant, as well as the degree to which they are dominant and the form in which dominance is expressed. A new invader might expand to a monotype.

By definition, dominant species control their habitat and the presence and performance of other species. However, due to the difficulty of assessing "control," a more general definition assigns dominance to the most abundant species (Carpenter 1956, Greig-Smith 1986). Simply naming a dominant species provides little information about a community or its condition. Identifying different forms of dominance, however (as Rabinowitz 1981 described for rarity), could give information about the condition of a community. We created a dominance index that combines three easily measured attributes of a species in a particular location to determine which species are dominant and assigned different forms of dominance to those species.

Because our dominance index uses context dependent attributes, shifts in dominance form could help characterize different wetlands and allow comparisons across space and time. We used our dominance index to determine the dominant species in each of 72 Great Lakes coastal wetlands and assigned a form of dominance to each. We hypothesized that: (1) species would show different forms of dominance in different locations, and; (2) dominance forms could be associated with anthropogenic stress.

Methods

Investigators for the Great Lakes Environmental Indicators project (GLEI) collected vegetation data to develop indicators of wetland condition for Great Lakes coastal wetlands. Three sampling teams (see acknowledgments) collected data from 72 wetlands that represent a random sample of all U.S. Great Lakes coastal wetlands stratified to include a gradient of environmental conditions and three geomorphic types, coastal, riverine and protected (Danz et al. unpublished manuscript). In each wetland, the cover of plant species rooted in 1-m^2 quadrants was visually assessed. Data on environmental condition were collected by GLEI investigators and reduced using principle components analysis. We used the principle components scores from the first axis in four categories—agriculture, land cover, population density and point source pollution—as integrated measures of anthropogenic stress. (Danz et al. unpublished manuscript).

Our dominance index (DI) was modeled after Curtis and McIntosh's (1951) importance value. We used the GLEI database to derive three variables: tendency toward high cover, mean species suppression, and mean cover. Tendency toward high cover (THC) is a ratio of the number of times a species is "influential" in a plot, i.e. having > 25% absolute cover and the most cover, to the number of times it is present in a plot. Mean species suppression (MSS) is the mean of the inverse of the number of species (1/number of species) in a plot where the species of interest is "influential." Mean cover (MC) is the average cover of a species. The dominance index (DI) is computed as the average of the three variables. We computed DI for species that we considered to be potentially dominant based on two criteria. Potentially dominant species must be "influential" in at least one plot and be present in at least 1/3 of the plots in a wetland of interest.

After the DI was computed for each of the potentially dominant species, we selected dominant species using mean DI as a cut-off. Species with DI above the mean were dominant. Then, using the mean value as a cut-off to dichotomize each of the three components of the DI into "high" and "low" values, we differentiated seven forms of dominance comparable to Rabinowitz's (1981) seven forms of rarity (Table 1). In this way, we assigned a dominance form to each occurrence of a dominant species.

Table 1. Framework for 7 forms of dominance based on the dichotomization of 3 attributes.

	MSS High		MSS Low	
	MC High	MC Low	MC High	MC Low
THC High	1. Monotype	3. Compressed	5. Matrix	7. Patchy
THC Low	2. Ubiquitous	4. Aberrant	6. Diffuse	not dominant

Results and Discussion

For vegetation data in the GLEI database, mean DI found 35 species to be dominant. Eighteen showed monotype form, 4 showed ubiquitous form, 12 showed compressed form, 2 showed aberrant form, 14 showed matrix form, 1 showed diffuse form, and 13 showed patchy form. Monotype form and matrix form were the most common dominance forms among species that were dominant in four or more wetlands. Invasive *Typha* (*Typha angustifolia* L. and *Typha* x *glauca* Godr. combined), *Carex stricta* Lam., *Phalaris arundinacea* L. and *Calamagrostis canadensis* (Michx.) P. Beauv. showed monotype form more often than matrix form with monotype to matrix form ratios of 14:3, 2:1, 2:1 and 4:3, respectively. *Carex lasiocarpa* Ehrh. subsp. *americana* (Fernald) D.Löve & Bernard and *Carex lacustris* Willd. showed matrix form more often than monotype form with monotype to matrix form ratios of 1:5 and 1:3, respectively. However, *Myrica gale* L., a shrub, did not show monotype form in any wetland. *Impatiens capensis* Meerb., an annual, never showed matrix form (Fig. 1).

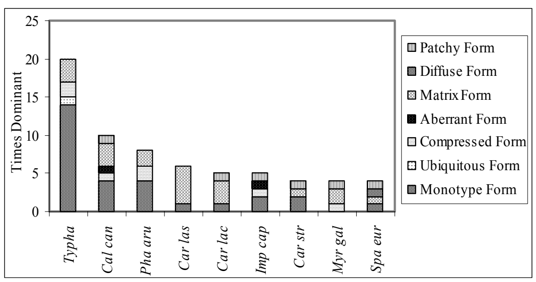

Figure 1. The number of times a species showed the seven forms of dominance. Species names are abbreviated using the first 3 letters of the genus and species.

Our results support our first hypothesis; individual species showed different dominance forms in different locations. For example, *Calamagrostis canadensis* showed five forms among ten wetlands and *Sparganium eurycarpum* showed a different form in each of the four wetlands in which it was dominant. However, some species predominantly displayed one form. Invasive *Typha* showed monotype form in 14 of the 20 wetlands in which it was dominant, and *Carex lasiocarpa* showed matrix form in 5 out 6 (Fig. 1). Thus, dominant form was a function of both species and location.

Our second hypothesis, that forms of dominance can be associated with anthropogenic stress, is also supported by our results. A Kruskal-Wallis test showed that the median stressor scores for wetlands in which different dominance forms occurred were significantly different in the agriculture ($P = 0.005$), land cover ($P = 0.008$) and point source ($P = 0.052$) categories, but not in the population density category ($P = 0.215$). Based on Mann-Whitney pair-wise tests, matrix form occurred in wetlands that have lower nutrient input from agriculture than monotype form, were surrounded by more forested land than monotype and compressed forms, and had lower loading from point sources than compressed form. On the other hand, compressed form occurred in wetlands that were surrounded by more agricultural land than patchy and matrix forms, and had higher loading from point sources than matrix form. Similarly, monotype form occurred in wetlands with higher nutrient input from agriculture and that were surrounded by more agricultural land than matrix form.

Other studies have shown changes in the behavior of dominant species with anthropogenic stress. Werner and Zedler (2002) showed that wet meadows with heavy sedimentation had low species richness and speculated that the sediment disadvantaged native sedges while it gave *Phalaris arundinacea* an advantage. This pattern was then demonstrated experimentally by Kercher and Zedler (2004). Similarly, Woo and Zedler (2002) showed an increase in density and height of *Typha* x *glauca* with fertilizer additions, but no response by *C. stricta*. Differences in forms of dominance across wetlands and/or changes in form over time may indicate differences and changes in abiotic attributes of communities such as nutrient availability and sediment addition.

While differences were significant, dominance forms showed much overlap in the stressor scores of wetlands in which they occurred. The characteristics of individual dominant species could account for the wide variation in stressor scores associated with a given dominance form. In addition, the stressor variables that contributed to the stressor scores were computed for a large area surrounding each wetland, and the precise relationship between them and the wetland is unclear. Direct environmental sampling would be required to directly relate species, anthropogenic stress and forms of dominance. Differences in wetland setting unrelated to anthropogenic stress, like climate and geomorphology, might also influence dominance forms.

We suggest that the use of DI as an indicator would have an advantage over simply tracking changes in the identity of dominant species. As conditions in coastal wetlands change, DI and the form of dominance would also be expected to change. As human development increases, nutrient and sediment inputs and hydroperiods also change. In the long term and at a large scale, global climate change alters weather patterns. Coastal wetland species will respond to such changes, and dominance forms will likely shift, either because the behavior of the dominant species changes or because other species become dominant. Our DI can track changes in dominance form, indicating changes beyond those assessed by diversity indices and composition.

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