Contributed Paper

Invasion, Disturbance, and Competition: Modeling the Fate of Coastal Plant Populations

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Abstract: *Wetland habitats are besieged by biotic and abiotic disturbances such as invasive species, hurricanes, habitat fragmentation, and salinization. Predicting how these factors will alter local population dynamics and community structure is a monumental challenge. By examining ecologically similar congeners, such as* Iris hexagona *and* I. pseudacorus *(which reproduce clonally and sexually and tolerate a wide range of environmental conditions), one can identify life-history traits that are most influential to population growth and viability. We combined empirical data and stage-structured matrix models to investigate the demographic responses of native (*I. hexagona*) and invasive (*I. pseudacorus*) plant populations to hurricanes and salinity stress in freshwater and brackish wetlands. In our models* I. hexagona *and* I. pseudacorus *responded differently to salinity stress, and species coexistence was rare. In 82% of computer simulations of freshwater marsh, invasive iris populations excluded the native species within 50 years, whereas native populations excluded the invasive species in 99% of the simulations in brackish marsh. The occurrence of hurricanes allowed the species to coexist, and species persistence was determined by the length of time it took the ecosystem to recover. Rapid recovery (2 years) favored the invasive species, whereas gradual recovery (30 years) favored the native species. Little is known about the effects of hurricanes on competitive interactions between native and invasive plant species in marsh ecosystems. Our models contribute new insight into the relationship between environmental disturbance and invasion and demonstrate how influential abiotic factors such as climate change will be in determining interspecific interactions.*

Keywords: clonal plants, exotic species, extinction, habitat disturbance, hurricanes, *Iris hexagona*, *I. pseudacorus*, matrix models, population dynamics, species competition

Invasión, Perturbación y Competencia: Modelando el Destino de Poblaciones de Plantas Costeras

Resumen: *Los hábitats de humedales están acosados por perturbaciones bióticas y abióticas como las especies invasoras, huracanes, fragmentación de hábitat y salinización. La predicción de cómo estos factores alterarán la dinámica poblacional y la estructura de la comunidad es un reto monumental. Mediante el examen de congéneres similares ecológicamente, como* Iris hexagona *e* I. pseudacorus *(que se reproducen por clones y sexualmente y toleran un amplio rango de condiciones ambientales), se pueden identificar características de la historia de vida que son más influyentes en el crecimiento y la viabilidad poblacional. Combinamos datos empíricos y modelos matriciales estructurados por estadios para investigar las respuestas de las poblaciones de plantas nativas (*I. hexagona*) e invasoras (*I. pseudacorus*) a huracanes y estrés por salinidad en humedales de agua dulce y salobre. En nuestros modelos,* I. hexagona *e* I. pseudacorus, *respondieron de manera diferente al estrés por salinidad y la coexistencia de las especies fue rara. En 82% de las simulaciones en computadora del humedal dulceacuícola, las poblaciones invasoras excluyeron a las especies nativas en un plazo de 50 años, mientras que las poblaciones nativas excluyeron a la especie invasora en 99% de las simulaciones de humedal salobre. La ocurrencia de huracanes permitió la coexistencia de las especies, y la persistencia de las especies estaba determinada por el tiempo que tomaba la recuperación del ecosistema. La recuperación rápida (2 años) favoreció a la especie invasora, mientras que la recuperación gradual (30 años) favoreció a la especie nativa. Se sabe poco sobre los efectos de los huracanes sobre las interacciones competitivas entre*

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especies de plantas nativas e invasoras en ecosistemas de marisma. Nuestros modelos aportan una nueva perspectiva de las relaciones entre la perturbación ambiental y las invasiones y demuestran la influencia de factores abióticos, como el cambio climático, en la determinación de interacciones interespecíficas.

Palabras Clave: competencia de especies, especies exóticas, dinámica poblacional, extinción, huracanes, *Iris hexagona*, *I. pseudacorus*, modelos matriciales, perturbación de hábitat, plantas clonales

Introduction

Invasive species can devastate the ecological health and economic value of ecosystems (Williamson 1996; Williamson & Fitter 1996). Many factors influence the spread of exotic species (Lonsdale 1999), including light (Keane & Crawley 2002), fire (Hierro et al. 2006), nutrients (Lake & Leishman 2004), natural enemies (Davis et al. 2000), and management practices (Chmura & Sierka 2007). Some exotic species have higher population growth rates than native populations (Loehle 1987) and thus a greater potential to rapidly colonize available habitat (Taylor et al. 2004). Despite numerous studies investigating life-history traits and population dynamics (Davis et al. 2006; Meiners 2007; Van Kleunen & Johnson 2007), no consensus has emerged to predict precisely why or when a colonization event becomes an invasion (Zedler & Kercher 2004; Sebert-Cuvillier et al. 2007). Progress in invasion biology has been frustrated in part because of complex and idiosyncratic interactions between the life-history traits of exotic species and abiotic features of the colonized environments (Williamson & Fitter 1996; Davis et al. 2000).

Coastal wetlands are disproportionately affected by invasive species relative to other ecosystems (Stephens & Sutherland 1999; With 2002). They encompass 6% of the Earth's surface (Mitsch & Gosselink 1993) but harbor 24% of the most destructive plants (Zedler & Kercher 2004). As sea levels rise with changing global climate, wetlands become ever more fragmented (Michener et al. 1997; Sanchez Sanchez & Islebe 1999; Goldenberg et al. 2001), presenting even greater opportunities for exotic colonists with rapid reproductive rates (Davis et al. 2000; Brown & Mitchell 2001; Marvier et al. 2004). Wetlands along the Gulf of Mexico are particularly vulnerable to tropical storms, which can produce catastrophic wind damage and force large quantities of salt water into freshwater ecosystems. Much of the destruction by Hurricane Rita (2005) resulted from saltwater inundation of inland vegetation (Guidroz et al. 2007). Little is known about how such disturbance affects invasive species, although results of some studies suggest that invasives, such as *Pittosporum undulatum* populations in Jamaica (Bellingham et al. 2005), can benefit because they are better at exploiting recently disturbed or fragmented habitats than native species (Rejmanek & Richardson 1996; Horvitz et al. 1998; Keitt et al. 2001).

Quantitative models are valuable tools for conservation biology and can be applied to a wide variety of ecological concerns (Caswell 2001; Weppler et al. 2006; Ackleh et al. 2007). In particular, stage-structured matrix models can pinpoint crucial life-stage responses to the abiotic environment (Pascarella & Horvitz 1998; Garcia 2003; Thomson 2005) and invasive species (Shea & Kelly 1998, 2004; Parker 2000). We used this approach to examine the responses of single-species and mixed-species populations of native (*Iris hexagona*) and invasive (*I. pseudacorus*) plants to environmental variation and disturbance in the Louisiana wetlands of the northern Gulf of Mexico.

The Louisiana blue flag iris (*I. hexagona* [Iridaceae]) has been studied for decades by botanists, ecologists, and evolutionary biologists (Viosca 1935; Cruzan & Arnold 1993; Meerow et al. 2005). Most irises are glycophytes, but several species, including *I. hexagona* and *I. pseudacorus*, populate freshwater (0–0.2 g NaCl/L) and brackish (approximately 1.0–8 g NaCl/L) habitats. Salt causes severe physiological stress in freshwater plants (Hasegawa et al. 2000; Xiong & Zhu 2002). Even among *I. hexagona* populations adapted to brackish conditions, salinity alters endogenous hormones (Wang et al. 2001), reproductive mode (Van Zandt et al. 2003), flowering phenology (Van Zandt & Mopper 2002), leaf senescence (Schile & Mopper 2006), seed germination (Van Zandt & Mopper 2004), florivory (Geddes & Mopper 2006; Tobler et al. 2006), and herbivory (Wang & Mopper 2008). Thus, the ability of a species to tolerate salt will play an increasingly important role in the long-term persistence of iris and other plant populations in coastal environments.

The introduced yellow flag iris (*I. pseudacorus*) provides an opportunity to investigate interactions between closely related and ecologically similar species. This Eurasian iris is indigenous to temperate freshwater and brackish marsh communities (Sutherland 1990; Sutherland & Walton 1990). It has attained pest status throughout North America (Raven & Thomas 1970) as an ecosystem engineer because its aggressive growth and rhizomatous mats uplift sediment, alter habitat, and diminish diversity of native species (Thomas 1980). *I. pseudacorus* is widely cultivated throughout southern Louisiana and naturalized clonal patches are expanding into culverts, bayous, and lakes near coastal areas (K. Wiens & S.M., unpublished data). The damage caused by *I. pseudacorus* to ecosystems elsewhere in North America underscores its potential threat to Louisiana wetlands, and native species

such as *I. hexagona*. We developed quantitative models to examine the responses of and interactions between *I. hexagona* and *I. pseudacorus* in the Louisiana Gulf Coast. Such efforts can elucidate how climate change, hurricanes, and saltwater intrusion affect invasion dynamics.

Methods

Iris Life Cycle

The iris life cycle has 4 stages: seeds (*s*), seedlings (*l*), flowering adult ramets (*f*), and belowground rhizomes (*r*) (Fig. 1). We used the functions $N_s(t)$, $N_l(t)$, $N_f(t)$, and $N_r(t)$ to denote the number of individuals in each of the respective life-cycle stages at time *t*. Transitions between stages are annual. For the aboveground stages, $0 < p_i \leq 1$, where *p* is the proportion of surviving plants in stage *i* ($i = 1, 2$) at time *t* that move into the subsequent stage at time $t + 1$ (i.e., in 1 year). Thus $1 - p_i$ is the proportion of individuals in stage *i* that remain in the original

Figure 1. The 4-stage life cycle of I. hexagona *and* I. pseudacorus. *Solid lines indicate stage transitions:* $N_s(t)$, *number of seeds at time* t *supplemented by the number of seeds (b) produced by an adult ramet;* p_1s_1, *transition probability from seeds to seedlings;* $(1 - p_1)s_1$, *seeds that remain in the seed bank;* p_2s_2, *transition probability from seedlings into flowering adults;* $(1 - p_2)s_2$, *proportion of seedlings that remain in an asexual nonflowering condition;* c_1, *number of rhizomes formed by adults;* p_3, *proportion of rhizomes that produce flowering adults;* s_3, *rhizome survival;* $N_r(t)$, *total number of rhizomes at time* t.

stage. Iris seeds are water dispersed and typically germinate on the soil surface. We denoted the proportion of seeds that developed into seedlings as p_1 and the proportion of seedlings that entered the flowering stage as p_2. The survival rate of seeds was s_1, and the survival rate of seedlings was s_2. Thus, the transition between stages was the product of 2 independent parameters: the probability of surviving a given stage (s_i) and the probability of moving to the next stage (p_i) (Getz & Haight 1989).

In our model ramets flowered only once and generated a rhizome that produced a new flowering ramet. Floral shoots are monocarpic, reproduce once only, and seeds are produced once each year. Thus, *b* represented the number of viable seeds produced by one flowering ramet at time *t* that survive to $t + 1$. In the belowground stage, p_3 was the proportion of rhizomes that produce flowering ramets at time *t*, which survive to $t + 1$. The number of rhizomes produced by 1 flowering ramet at time *t* that survive to $t + 1$ was denoted as C_1. Individuals could only move to a new stage once per year.

Matrix Population Model

The parameters in the matrix varied explicitly with salinity (fresh [0.0–0.2 g NaCl/L] vs. brackish [4–8 g NaCl/L]) and were derived from the empirical data described later (Table 1). The estimate for seed numbers at $t + 1$ included new seeds produced and seeds that survived in the seed bank from time interval *t*. For the seed stage, this resulted in the following: $N_s(t + 1) = (1 - p_1)s_1N_s(t) + bN_f(t)$, where $(1 - p_1)s_1$ is the proportion of viable seeds that fail to germinate into seedlings, but survive to $t + 1$; $bN_f(t)$ is the number of new seeds derived from flowers at stage (*t*) that survive to $t + 1$; and p_1s_1 is the proportion of seeds that germinate, enter the seedling stage at time *t*, and survive to $t + 1$.

The number of seedlings at time $t + 1$ was $N_l(t + 1) = p_1s_1N_s(t) + (1 - p_2)s_2N_l(t)$, where p_1s_1 is the proportion of seeds that germinate during *t*, form ramets, and survive to $t + 1$, and $(1 - p_2)s_2$ is the proportion of seedlings that remain in an asexual, nonflowering state and survive to time $t + 1$, with survival rate s_2. Similarly, the number of flowering ramets was described by $N_f(t + 1) = p_2s_2N_l(t) + p_3N_r(t)$, where p_2s_2 is the proportion of seedlings that enter the flowering stage at time *t* and survive to $t + 1$. Finally, p_3 was the proportion of rhizomes at time *t* that produce flowering ramets and survive to $t + 1$. Our model assumes each rhizome produces 1 flowering ramet that survives to $t + 1$. Annual survival rate of flowers was zero. Therefore, the number of rhizomes at time $t + 1$ was $N_r(t + 1) = c_1N_f(t) + s_3N_r(t)$, where c_1 is the number of rhizomes produced by flowering ramets that survive to $t + 1$, and s_3 is the survival rate of rhizomes that do not produce ramets in that year but remain dormant.
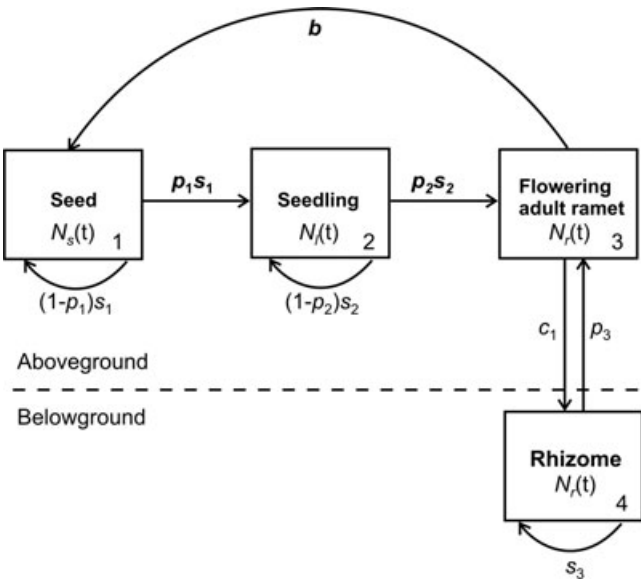
Table 1. Estimated transition parameters used in 1- and 2-species models of *I. hexagona* and *I. pseudacorus* populations colonizing freshwater and brackish wetlands.

Parameter	Symbol	*I. hexagona*		*I. pseudacorus*	
		Fresh	Brackish	Fresh	Brackish
No. of seeds produced by a ramet	B	117	186	276	276
Seed survival rate	s_1	0.7	0.4	0.6	0.4
Seedling survival rate	s_2	0.8	0.8	0.8	0.6
Rhizome survival rate	s_3	0.9	0.6	0.9	0.5
Seeds to seedlings	p_1	0.6	0.4	0.7	0.3
Seedlings to flowering ramets	p_2	0.8	0.6	0.7	0.4
Rhizomes that produce flowering ramets	p_3	0.6	0.8	0.5	0.4
Rhizomes produced by flowering ramets	c_1	2	1	2	1

In the 1- and 2-species models, the parameters p_1, s_2, p_3, s_3, c_1, and b were regulated by a density-dependent factor from the Beverton–Holt equation: $f(Z) = 1/(1+aZ)$. Here, $Z = N_l + N_f + N_r$ was the total number of individuals in the seedling, flowering, and rhizome stages. The constant a was set at 0.003 and pertained to an individual's response to density (Caswell 2001; Gaylord et al. 2005). Thus, $f(Z)$ took values in the interval (0, 1) for any iris density level Z. The constant a was estimated empirically by counting the number of ramets that reached carrying capacity in our experimental mesocosm populations (1.0 m^2) and extrapolating the number of individuals to a habitat size of 100 m^2.

Combining the above equations resulted in the following nonlinear matrix population model, $\mathbf{M}_1$:

$$N(t+1) = \begin{pmatrix} N_s(t+1) \\ N_l(t+1) \\ N_f(t+1) \\ N_r(t+1) \end{pmatrix}$$

$$= \begin{pmatrix} (1-p_1 f(Z))s_1 & 0 & bf(Z) & 0 \\ p_1 s_1 f(Z) & (1-p_2)s_2 f(Z) & 0 & 0 \\ 0 & p_2 s_2 f(Z) & 0 & p_3 f(Z) \\ 0 & 0 & c_1 f(Z) & s_3 f(Z) \end{pmatrix}$$

$$\times \begin{pmatrix} N_s(t) \\ N_l(t) \\ N_f(t) \\ N_r(t) \end{pmatrix} = M(N(t))N(t).$$

MODEL PARAMETERS

We based estimates of model parameters on field observations and the results of separate common garden and greenhouse experiments, of which some are published and some are ongoing. Plant growth and reproduction data were acquired from a 2-year experiment that estimated the effects of freshwater and brackish treatments on *I. hexagona* (Van Zandt et al. 2003). To summarize, we collected *I. hexagona* plants from 10 natural populations and used Instant Ocean (Aquarium Systems, Mentor, Ohio) to produce different levels of salinity (fresh, 3, and 6 g NaCl/L). Each population was replicated 3 times in each salinity treatment. Salt concentrations were selected that reflected natural field variation and were monitored regularly with an Orion 125 salinity meter (Orion Research, Beverly, Massachusetts).

Iris hexagona seed germination and survival was ascertained in a 2-year greenhouse experiment that exposed seeds to salinity levels ranging from 0 to 9 g NaCl/L (Van Zandt & Mopper 2004). In this experiment, we planted 5626 seeds individually in containers with vermiculite and randomly assigned 1 of 4 salinity treatments (0, 3, 6, and 9 g NaCl/L) to each one. Treatment salinities reflect the levels that occur in natural populations during flowering, seed development, and germination. *Iris hexagona* rhizome growth was estimated in an experiment conducted in 2005 with the methods described in Van Zandt et al. (2003) and unpublished data of S.P. and S.M. Plants collected from 3 wild populations were grown in 45 separate mesocosms and exposed to fresh, 4, and 8 g NaCl/L for 2 years. Survival rates for *I. hexagona* and *I. pseudacorus* were acquired from an ongoing common garden experiment in which rhizomes were planted in 96 separate mesocosms and randomly assigned to salinity treatments ranging from 0 to 8 g NaCl/L (K. Wiens, G. Goranova, & S.M., unpublished data), following methods described in Van Zandt et al. (2003). Seed production and germination rates of *I. pseudacorus* were determined by collecting from naturalized Louisiana populations and ongoing greenhouse and common garden experiments (K. Wiens, G. Goranova, and S.M., unpublished data) following the methods of Van Zandt and Mopper (2004) and Van Zandt et al. (2003).

We estimated freshwater and brackish vital rates (Table 1) by averaging values for *I. hexagona* and *I. pseudacorus* performance in 0 and 4–6 g NaCl/L. In freshwater, *I. pseudacorus* ramets grew more vigorously and had higher fertility than *I. hexagona* (mean = 276 and 117 seeds/ramet, respectively). In brackish conditions, *I. hexagona* produced more seeds ($n = 186$ per ramet).

We did not have data for *I. pseudacorus* seed production in brackish conditions; thus, we used the value for freshwater conditions ($n = 276$ seeds/ramet) in the model. Although established with identical rhizome biomass, invasives grew rapidly and excluded native plants in freshwater treatments, but had weaker growth than *I. hexagona* in brackish conditions (K. Wiens, G. Goranova, & S.M., unpublished data).

Because we obtained vital rates from several independent experiments conducted at different time periods, which increased spatial and temporal variation in the estimates, we provide vital rates only to a precision of 10%. In addition, simulations used a range of ±20% of the original parameter values. We are currently conducting a comprehensive common-garden experiment that will test our proposed models with empirical data and allow us to refine parameters and transition values if needed.

SINGLE-SPECIES SIMULATIONS

We first simulated population growth for each species separately with estimated vital rates (Table 1) in matrix $\mathbf{M}_1$. Simulated populations were established with either a single seed or rhizome propagule in an uninhabited freshwater or brackish wetland (area arbitrarily designated as 100 m^2). We ran simulations for 30 time steps, with each step representing 1 year (MATLAB, Mathworks 2007). To identify life-stage parameters that strongly influence population growth (Kalisz & McPeek 1992; Caswell 2001; Davis et al. 2004*b*), we calculated the relative change in λ (the intrinsic rate of population growth) caused by altering individual matrix elements. This was estimated as $e_{ij} = (m_{ij}/\lambda) \times (\partial\lambda/\partial m_{ij})$, where e_{ij} is the elasticity value for the element m_{ij} (i.e., the element in the *i*th row and *j*th column) of the inherent projection matrix $\mathbf{M}(0)$.

MIXED-SPECIES SIMULATIONS

To predict the population dynamics of co-occurring native and invasive irises in freshwater and brackish habitats, we ran simulations with the following model $\mathbf{M}_2$ that represents both species growing in a single patch:

$$\begin{pmatrix} N^{native}(t+1) \\ N^{invasive}(t+1) \end{pmatrix} = \begin{pmatrix} M^{native} & 0 \\ 0 & M^{invasive} \end{pmatrix} \begin{pmatrix} N^{native}(t) \\ N^{invasive}(t) \end{pmatrix}.$$

The model was parameterized using the vital rate estimates (Table 1). The 2-species matrices $\mathbf{M}^{native}$ and $\mathbf{M}^{invasive}$ contained the same elements as the 4×4 matrix for the single species, but the mixed-species populations were established with seed, not rhizome, propagules. Simulations ran for 50 years and included a density function for population growth of both species, such that *Z* is the total number of seedlings, flowering ramets, and rhizomes. *Iris hexagona* and *I. pseudacorus* did not contribute equally to *Z* because their vital rates vary in response to environmental conditions (Table 1):

$$Z = N_l^{native} + N_f^{native} + N_r^{native} + N_l^{invasive}$$
$$+ N_f^{invasive} + N_r^{invasive}.$$

COMPETITIVE EXCLUSION

We ran Monte Carlo simulations to establish the probabilities of competitive exclusion in freshwater and brackish conditions. Frequent stochastic shifts between brackish and fresh conditions are unlikely in iris habitat; thus, our simulations included only deterministic variation. Parameters for each run were sampled randomly from a normal distribution with vital rates varying ±20% from the mean parameter values of either a freshwater or a brackish habitat (Table 1). The distribution was truncated such that transition probabilities remained between 0 and 1. Sets of randomly selected parameters were fixed for individual time series, then new parameter values were randomly selected and the process repeated for each calculation. Ten thousand simulations were conducted to obtain probabilities that one species would exclude the other in an initially unpopulated freshwater or brackish wetland.

Impact of Hurricanes

Major tropical storms occur about once per decade along the U.S. Louisiana Gulf Coast, although frequencies appear to be increasing. In 2005 Hurricane Rita caused heavy mortality of iris populations (S.M., personal observation). Saltwater intrusion into freshwater habitat killed virtually all ramets, but populations are currently recovering by recruitment from the seed bank. To predict how periodic hurricanes might affect the coexistence of *I. hexagona* and *I. pseudacorus* in freshwater wetlands, we simulated a major hurricane salt pulse, followed by recovery periods of different length. Prehurricane populations were initially established with a single native and invasive seed in an unpopulated freshwater habitat and allowed to grow for 30 years, at which time we introduced the saltwater pulse. The pulse was set to cause seed and plant mortality of 90% for both species.

We examined 3 possible scenarios of how the time frame of hurricane recovery affects interspecific interactions between *I. hexagona* and *I. pseudacorus*. Following the hurricane salt pulse, irises in the rapid-recovery model experienced brackish vital rates for 2 years and then they were returned to freshwater vital rates (Table 1) until the next hurricane. Populations in the intermediate recovery group experienced brackish vital rates for 15 years after the hurricane and then returned to freshwater vital rates until the next event. And populations in the delayed recovery group experienced brackish vital rates for 30 years after the hurricane and then they were returned to freshwater vital rates until the next event.
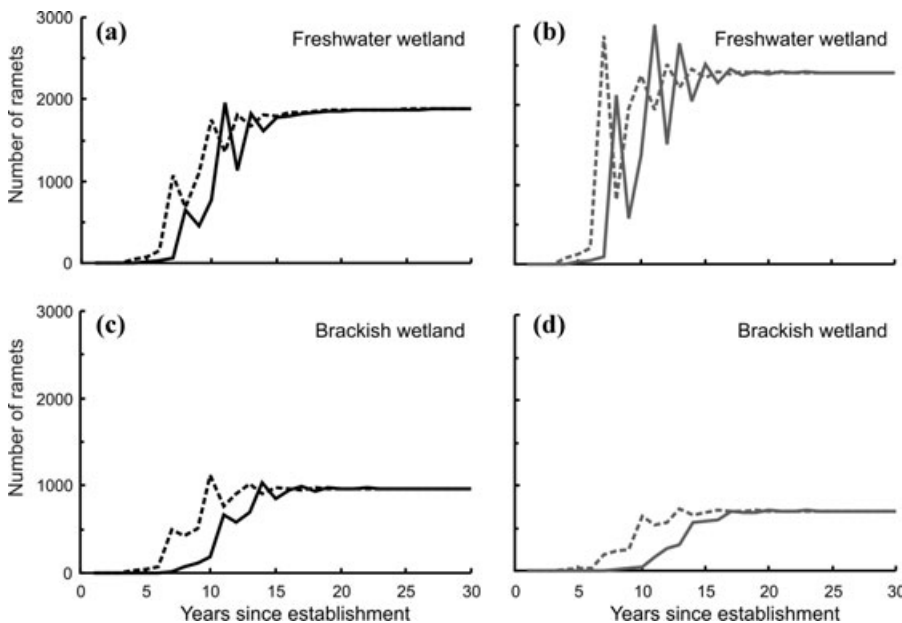
These scenarios reflect potential temporal differences in recovery from hurricanes in Gulf Coast wetlands. Unless precipitation is high, soils retain NaCl for long periods. Droughts can exacerbate salt retention. Nevertheless, abundant precipitation and snow melt can facilitate rapid reversion to freshwater conditions.

Results

Monospecific Populations

Species identity and habitat strongly influenced population growth, whereas propagule type had a weaker effect. Populations founded by rhizomes exhibited a higher initial rate of growth than populations founded by seeds, but the difference disappeared within about 15 years (Fig. 2). Both species attained higher densities in freshwater (Figs. 2a & 2b) than in brackish habitats (Figs 2c & 2d). *Iris pseudacorus* populations reached higher densities than *I. hexagona* in freshwater habitats (Figs 2a & 2b), but in brackish habitats, *I. hexagona* population densities were higher (Figs 2c & 2d).

The parameters most influential to population growth (λ) were similar in the 2 species. Fertility (*b*, the number of seeds) was the most important factor in fresh and brackish habitats, contributing 28.5 and 27.8%, respectively, to *I. hexagona* and 30.5 and 27.9%, respectively, to *I. pseudacorus* population growth. In contrast, clonal reproduction in fresh and brackish habitats contributed 4.5 and 4.4%, respectively, to *I. hexagona* and 2.3 and 3.0%, respectively, to *I. pseudacorus* population growth.

Competitive Exclusion

Responses of vital rates to environmental salinity strongly influenced competitive interactions between *I. hexag-*

ona and *I. pseudacorus* (Fig. 3). The dominant eigenvalue (λ) of the inherent projection matrix was the following for each species–condition combination: freshwater wetland *I. hexagona* = 3.4619, freshwater wetland *I. pseudacorus* = 4.2585, brackish wetland *I. hexagona* = 2.7384, and brackish wetland *I. pseudacorus* = 2.2846. Invasive *I. pseudacorus* populations grew faster in freshwater habitats, eventually excluding *I. hexagona* within 30 years (Fig. 3a), whereas *I. hexagona* populations excluded *I. pseudacorus* within about 20 years in brackish wetlands (Fig. 3b). There was an 82% probability that invasive irises would exclude natives in freshwater habitat, in contrast with a 99% probability that native irises would exclude invasives within brackish habitats.

Impact of Hurricanes

The periodic salt pulses produced by hurricanes in freshwater marsh strongly affected the fate of *I. hexagona* and *I. pseudacorus* populations. Population densities and probability of coexistence varied in response to how rapidly the habitat returned to freshwater conditions following the storm salt pulse. When freshwater conditions returned rapidly (in 2 years), *I. pseudacorus* dominated and eventually excluded *I. hexagona* (Fig. 4a). In contrast, *I. hexagona* eventually excluded *I. pseudacorus* when brackish conditions persisted for 30 years after the storm (Fig. 4c). Coexistence of *I. hexagona* and *I. pseudacorus* occurred when hurricane recovery was intermediate (15 years, Fig. 4b). All simulations included a Beverton-Holt density-dependent factor (a) of 0.003; however, the field populations may display species and environmental variation that produce different density constants (e.g., Fig. 5).
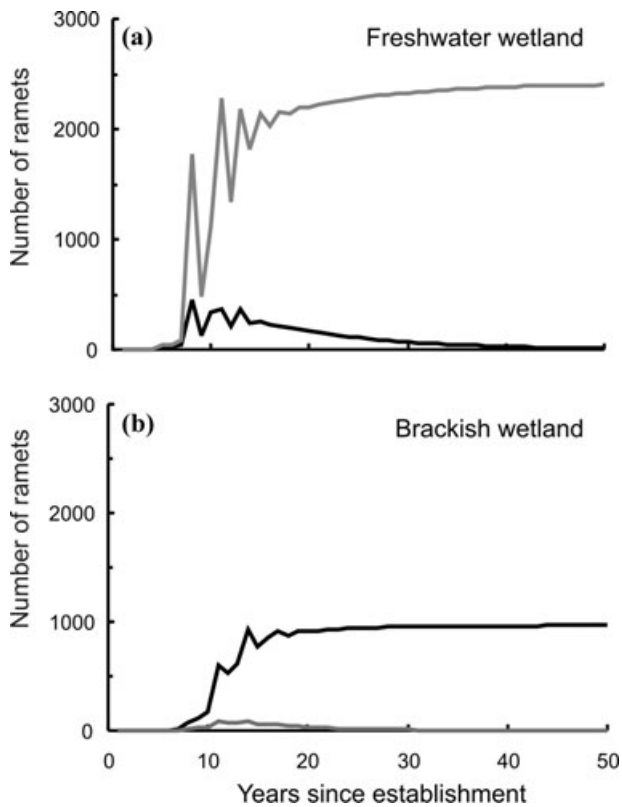
Figure 3. Population growth of co-occurring I. hexagona *and* I. pseudacorus *when established by seed in (a) freshwater (0.0–0.2 g NaCl/L) and (b) brackish (4–6 g NaCl/L) habitats (black line,* I. hexagona *seed; gray line,* I. pseudacorus *seed). Responses derived from vital rates in Table 1.*

Discussion

Habitat conditions strongly affected the population dynamics of *I. hexagona* and *I. pseudacorus*. In brackish conditions, the native species achieved the highest population growth rate and density, whereas the invasive species performed best in freshwater conditions. Although many invasive species possess life-history traits that promote spread, they often cannot proliferate because resources such as water, nutrients, and space limit establishment (e.g., Eriksson & Ehrlén 1992; Lake & Leishman 2004; Gotelli & Ellison 2006), particularly in the critical colonization phase (Drake & Lodge 2006). In fact, only a small proportion of exotic species are thought to become invasive (Williamson 1996; Williamson & Fitter 1996) because unsuitable conditions hamper recruitment (Richardson & Williams 1994; Wang & Wang 2006).

Our results indicated sexual reproduction was the most important parameter for population growth in *I. hexagona* and *I. pseudacorus*. Indeed, seeds may be the primary source of population revival following hurricane disturbance. Nevertheless, *I. hexagona* and *I.*
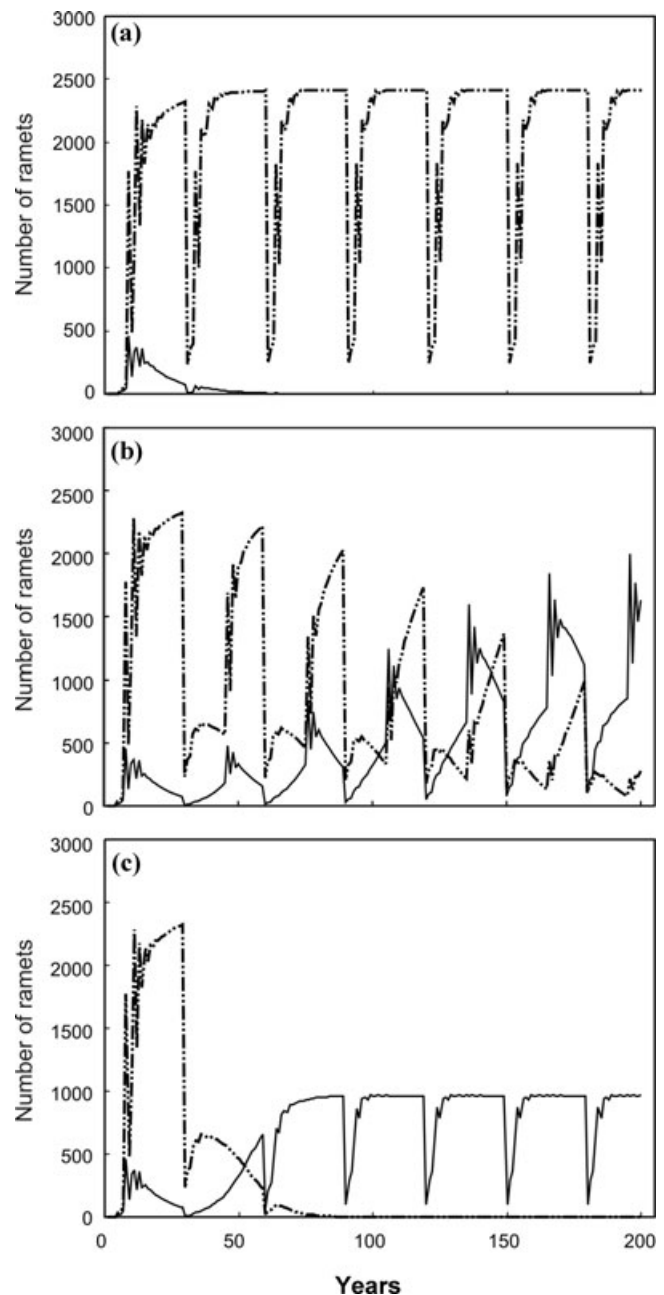

Figure 4. Effects of periodic hurricanes on competitive interactions between I. hexagona *(solid line) and* I. pseudacorus *(hatched line). Three periods of recovery of the system to freshwater conditions are illustrated: (a) 2 years, (b) 15 years, and (c) 30 years. Species coexist in the 15-year recovery scenario.*

pseudacorus also propagate clonally, and their mixed reproductive strategy may buffer against environmental disturbance (Stuefer 1998; Xiaoa et al. 2006), as seen in *Fragaria chiloensis*, where belowground networks offset environmental disturbance (Holzapfel & Alpert 2003). When seed production fails because of florivory (Tobler et al. 2006) or a scarcity of pollinators (Davis
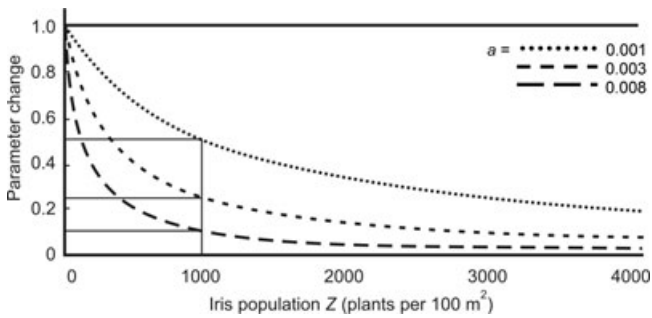
Figure 5. The effect of the constant a *in the Beverton–Holt density function f(Z) = 1/(1+*aZ*) for each density-dependent parameter in the model M1. A value of 0 (solid line) indicates population density does not affect the examined parameter.*

et al. 2004*a*, 2004*b*), clonal reproduction can sustain population growth and reduce the possibility of extinction (Fischer & Matthies 1998; Willi et al. 2005).

In our models, *I. hexagona* and *I. pseudacorus* rarely coexisted, and each species favored a different type of habitat. Invasives excluded natives in about 82% of encounters in freshwater habitats, whereas natives excluded invasives in 99% of encounters in brackish marsh. Surprisingly, the presence of hurricanes allowed the species to coexist. Following simulated hurricane salt pulses, subsequent brackish conditions, and eventual recovery to freshwater in 15 years, *I. hexagona* and *I. pseudacorus* coexisted for at least 200 years. The coexistence probability was determined by the duration of the recovery to original freshwater conditions. Rapid recovery (2 years) favored the invasive, whereas gradual recovery (30 years) favored the native.

Little is known about the effects of hurricanes on competitive interactions between native and invasive plant species in marsh ecosystems, and most research so far has occurred in tropical hammocks and forests (Horvitz et al. 1995). The prevailing view is that hurricanes accelerate invasion by harmful species (Horvitz et al. 1998; Rathcke 2001), but there are too few studies for a consensus. Although the actual incidence of hurricanes and the duration of recovery between them will be less regular than in our models, these simulations are a good starting point for more complex scenarios and indicate how influential abiotic factors such as climate change will be in determining interspecific interactions. Our models contribute new insight into the relationship between environmental disturbance and invasion (Stohlgren et al. 2001; Lake & Leishman 2004; Thompson et al. 2007) and indicate that population dynamics are influenced not only by the type of disturbance but by the frequency and timescale of ecosystem recovery.

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