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# Toward a Resilience-Based Conservation Strategy for Wetlands in Puerto Rico: Meeting Challenges Posed by Environmental Change

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## Abstract

Designing conservation strategies in human-dominated landscapes is challenging, owing to complex human-natural systems and evolving societal values. To meet this challenge, a robust, adaptive strategy should have a process for flexible implementation of incremental actions. We describe a hypothetical example for the Rio Grande de Arecibo watershed and coastal wetlands in Puerto Rico to address the first component. The process begins by identifying shared stakeholder objectives. This process benefits from a review of foundational research and knowledge base that includes global forcings and vulnerability of resources of interest. Forcings include climate change and pervasive urban sprawl. We focus on two taxonomic groups with differing life histories but strong dependence on water resource dynamics, another resource valued by humans. We stipulate objectives and multiple actions, but focus on those pertaining to hydro-management as the common thread in our example. We advanced two decision contexts of contrasting complexity, illustrated links between objectives and actions, and highlighted trade-offs triggered by varying resource valuation. Our focus was to highlight various components necessary to frame a resilience-based strategy, but we cannot overemphasize the importance of accommodating institutional and stakeholder changing priorities and values to ensure its successful implementation.

**Keywords** Adaptation strategies · Coastal wetlands · Decision models · *Eleutherodactylus* spp. · Puerto Rico · Resiliency · *Sicydium* spp. · Vulnerability · Watershed

## Introduction

The conservation challenges posed by climate and land use change are myriad and complex. Decision makers face the prospect of threats whose strength and periodicity are driven by exogenous factors outside of their control, with the most prominent examples being land use change and climate change. Yet, they are charged with predicting local or regional consequences and making decisions for systems whose responses could operate through multiple, sometimes interdependent, temporal and spatial processes and pathways (Conroy et al. 2011; Wise et al. 2014). Ultimately, the scale and rate at which land and seascapes are being modified is a primary concern to natural resource conservationists because it undermines species persistence and may result in homogenized biological communities and loss of ecological services (Gascon et al. 1999; Blair 2001; Fahrig 2003; Urban 2015; Aronson et al. 2016).

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The Caribbean Islands are considered a regional hotspot of biodiversity (Brooks et al. 2002), but it is also a region characterized by extensive human-induced changes (Martinuzzi et al. 2007; Radeloff et al. 2015; Gould et al. 2017). In Puerto Rico, forest cover decreased to less than 10% of its pre-European colonization extent by the 1930s as lands were cleared for agriculture, but has increased from 32% in 1990 to 57% in 2004 with the transition from an agricultural to an industrial and service-based economy (Birdsey and Weaver 1987; Lugo and Helmer 2004; Brandeis et al. 2007). Extensive deforestation contributed to the endangerment of avian species whose extinction rates were likely ameliorated by coffee cultivated under shade (Brash 1987, Gleffe et al. 2006, Irizarry et al. 2018). Mounting evidence suggests that changing climate is influencing the abundance and distribution of plants and animals in Puerto Rico (Jennings et al. 2014). Campos-Cerqueira and Aide (2017) reported the loss of 2 species of anurans and extirpation of 6 others from the lowlands of El Yunque National Forest, Puerto Rico, due to warming temperatures and disease. Similarly, 8 of 21 avian species have exhibited upward elevational shifts in distribution in the same forest (Campos-Cerqueira et al. 2017). In terms of societal values, hydrologic models suggested that at locations critical to water supply for human use, projected streamflow will be substantially below the projected withdrawals by 2099 (Van Beusekom et al. 2016).

Natural systems have an inherent ability to buffer against external forcings, largely gained over evolutionary time. This capacity, however, is undermined by the magnitude and frequency of disturbances if they take biological populations beyond their natural thresholds (Chazdon 2017; Falk 2017). When thresholds are not exceeded, interactions among several drivers of anthropogenic-induced change may generate multiple feedbacks with equally adverse consequences. In the aftermath of such events, many ecosystem or population responses exhibit resiliency, defined as the ability of an ecological entity to recover its distribution, abundance or function to a pre-disturbance state (Hobbs and Suding 2009). With projected increases in the frequency of the most extreme events (e.g. intense hurricanes, Kossin et al. 2017) or extreme conditions (e.g. drought, Hayhoe 2013), the conservation dilemma becomes whether to restore communities to their pre-disturbance condition using reference communities to guide recovery efforts, or allow the emergence of new or re-organized communities that may provide analogous functions and services (Lawler 2009; Chazdon 2017; Falk 2017).

Wise et al. (2014) reviewed several strategies designed to cope with changing environmental conditions and stressed the importance of framing a strategy that permits incremental implementation of adaptive actions to address proximal factors. Likewise, it is important for a strategy to accommodate evolving societal and institutional values and priorities (i.e., transformational stage) that might affect how incremental actions are selected and implemented. Both components, they argued,

are necessary for a robust, adaptive cycle and strategy. By this we mean, a structured, iterative process of robust decision making in the face of uncertainty, reduced over time through monitoring. Here we tackle the challenge of conservation in human-dominated landscapes by constructing an adaptive process for the flexible implementation of incremental actions at landscape levels in Puerto Rico (Fig. 1).

The iterative process includes problem framing, consideration of basic, foundational research, structuring the problem and decision models, and integrating planning, decision analyses and monitoring into the process so that scientific insights about the biological and cultural resources of concern, and the primary anthropogenic forcings that will impact the island, can facilitate learning and adaptation (Heller and Zavaleta 2009; Runge 2011). We outline multiple objectives and actions pertinent to our illustrative example, but focus on actions aimed at water resources. We developed two hypothetical decision contexts of different complexity that reflected available knowledge about the bio-cultural resources, and the potential tradeoffs that arise given system vulnerabilities and known and unknown uncertainties.

Our illustrative examples were designed for circumstances where the relevant stakeholders (e.g., Caribbean Landscape Conservation Cooperative) wish to conserve water and biological resources in the Rio Grande de Arecibo watershed and associated northern coastal wetlands (Fig. 2). The central role that water resources play in connecting the biological-cultural resources of value in this geography lead us to employ a watershed and wetlands-centered conservation strategy. Similar to the ‘ridge-to-reef’ concept (Rude et al. 2016), we seek to leverage the conservation benefits that accrue when a strategy is focused on actions that traverse the Rio Grande de Arecibo from its headwaters in the Cordillera Central mountain range to its outlet in the Atlantic Ocean, and the adjacent Sabana Seca wetlands (Fig. 2). From a biological perspective, our strategy was aimed to ensure the persistence of sustainable populations of two taxonomic groups with very distinct life history requirements that are bound together by their dependency on aquatic, mesic habitats. The first is *Eleutherodactylus* frogs, commonly known as coqui [co-Kee]. This group is a prime example of the tight evolutionary dependency between their abundance and distribution to mesic, micro-climatic environments (Joglar 1998). The second taxonomic group is an amphidromous fish genus, specifically, Sirajo Goby (*Sicydium* spp.), commonly known as cetí in its postlarval stage. Recent foundational research has shown that the Sirajo Goby’s amphidromous life history requires river-ocean connectivity and adequate river flow to complete early life-stage migrations (Kwak et al. 2016). Both taxonomic groups play important roles in energy transfer and ecological services (Beard et al. 2002, 2003; Engman et al. 2018; Valencia-Aguilar et al. 2013; Fitzsimons et al. 2003; Barbeyron et al. 2017; Kilham and Pringle 2000; March and Pringle 2011), and are valued culturally (Joglar 1998; Engman et al. 2018).

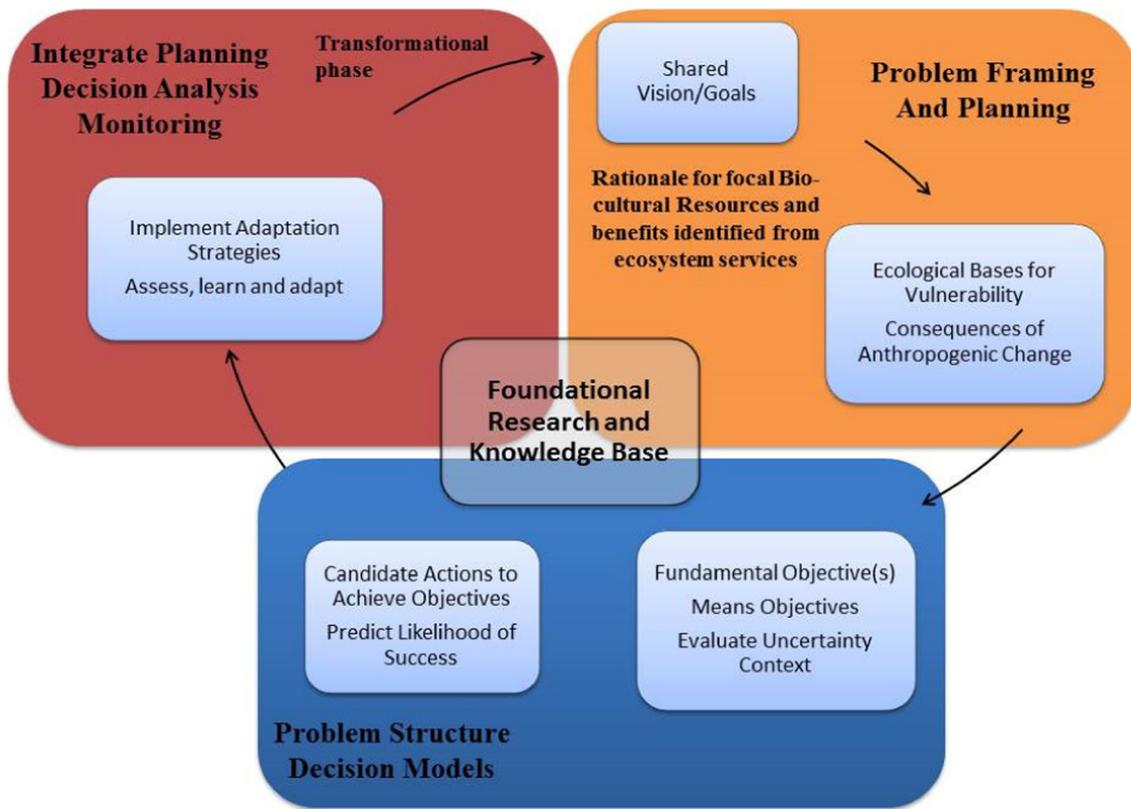


Fig. 1 Constructs of an incremental actions, resilience-based adaptive conservation strategy for a wetlands landscape in north-central Puerto Rico

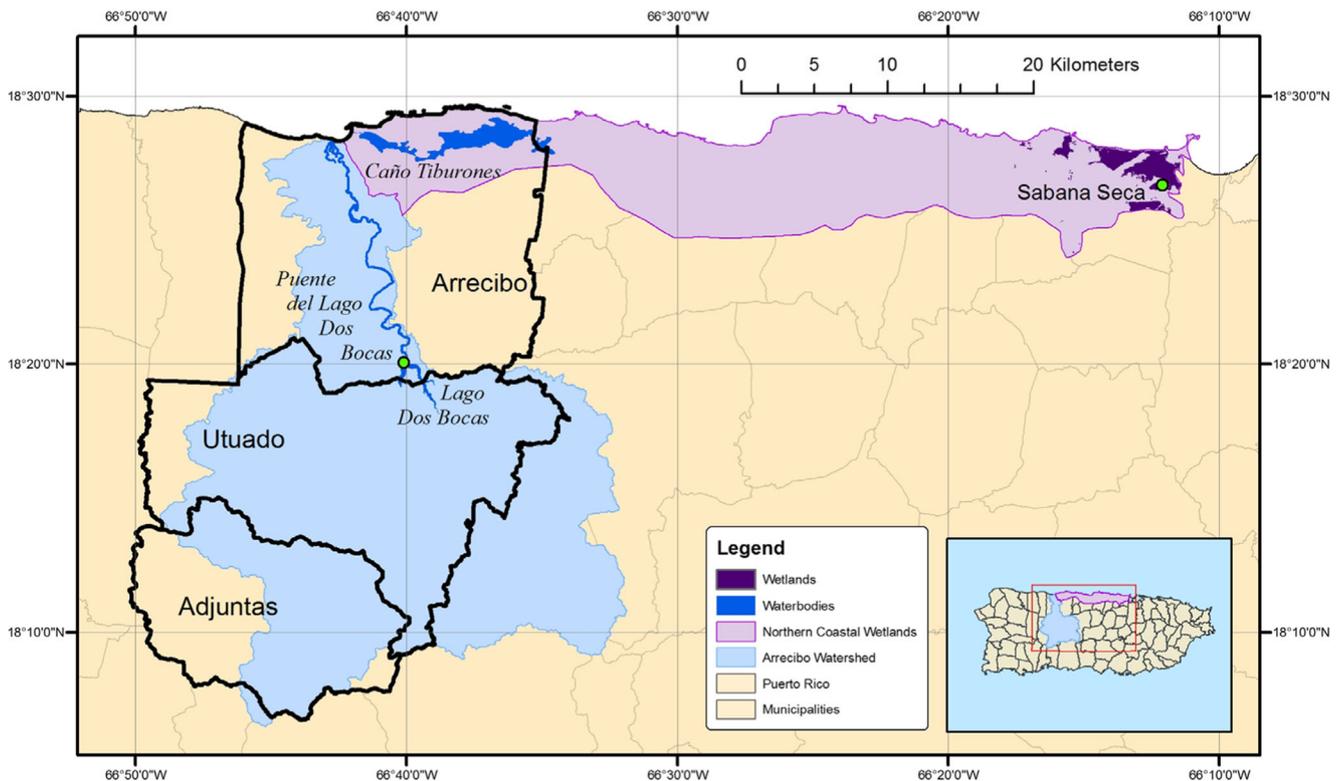


Fig. 2 Watershed of the Rio Grande de Arrecibo and selected northern coastal wetlands between the Rio Grande de Arrecibo and Sabana Seca, Puerto Rico

## Problem Framing and Planning

### The Watershed-Wetlands Conservation Nexus

The Rio Grande de Arecibo watershed complex has been singled out, most recently by the Caribbean Landscape Conservation Cooperative (<http://caribbeanlcc.org/landscape-conservation-design-pilot-areas/>), for its diverse flora and fauna and the many services it provides to human populations. Its headwaters are located in the mountains to the south of the town of Adjuntas. From there it flows north until it reaches the Atlantic Ocean, near the town of Arecibo. Water from the river is drawn for filtration, serving 5 municipalities (i.e., Utuado, Jayuya, Adjuntas, Arecibo, and San Juan). Stream waters are also used to generate hydroelectric power, and underground water flows discharge toward aquifers and support 6 types of coastal wetlands (i.e., lake, riverine, freshwater forested/shrub, freshwater emergent, estuarine, and marine). Coastal wetlands include the Caño Tiburones (1540 ha) and salt and fresh wetlands (e.g., Sabana Seca; Fig. 2).

There are several reasons why a wetland-watershed strategy has the potential to respond well to the challenges posed by multi-scale human dominance of the environment (Wise et al. 2014). First, it provides the means to conserve a naturally occurring habitat corridor that spans a gradient of biotic and abiotic strata. As such, the river itself becomes the center of the corridor to take advantage of: (1) the lower likelihood that human development activities will take place within or immediately adjacent to it, and (2), the diversity of “meso-climates” bisected by the river and adjacent wetlands that represent contiguous areas of lower climate change velocity (Loarie et al. 2009). The physiographic complexity of the watershed and wetlands also implies biogeochemical complexity that helps to preserve niche diversity and micro-scale climate *refugia* (Tingley et al. 2014; Morelli et al. 2016). The wetlands that bound and surround the river outlet further augment the ability of the river to act as a corridor by providing low-resistance dispersal opportunities for aquatic and other vagile species to more favorable climates, while lowering the risk of desiccation for mesic species in times of drought. Second, a water-centered strategy is critical for connecting species whose life stages span multiple aquatic and near-aquatic environments from marine, to brackish, to freshwater, and terrestrial (Kwak et al. 2016; Engman 2017). A watershed and wetlands approach also facilitates the provision of multiple benefits (i.e., ecosystem services) for stakeholder communities such as water filtration and water supply, flood control, agroforestry, and recreation (Massol González et al. 2006). Finally, linkages between wetland function and upland forest management also highlight the advantage of using a whole watershed-wetlands approach to allow for flexibility and diversity of management actions across space and time when tradeoffs exist between bio-cultural and economic objectives (Jones et al. 2018).

## Foundational Research and Knowledge Base

We begin with reviewing essential or seminal information on relevant anthropogenic forcings that decision makers may not have any ability to influence, but which nevertheless are the primary drivers of change in the watershed complex. We complement this process with a review of factors that might impinge on the two taxa of interest in the watershed complex (Fig. 1). This knowledge identifies area of opportunity and limiting factors that could be addressed through the implementation of selected actions. If relevant uncertainties are known and constrained, models may be used to predict consequences. However, if the decision making context is operating in a deep uncertainty environment (e.g. Lempert et al. 2004), other tools such as scenario or narrative building are likely to be more useful since attempts to place likelihoods and uncertainty bounds on specific outcomes could either suffer from overconfidence (Terando et al. 2016) or uncertainty estimates that are so wide as to be useless in the actual decision making process (Lempert 2002). As new knowledge accrues from parallel and often independent research efforts, opportunities for, and pace of, learning increase within all stages of the adaptive management cycle (Fig. 1).

**Climatic Changes** Anthropogenic (or human-caused) greenhouse gas emissions will result in rising temperatures in Puerto Rico as in the rest of the globe (Wuebbles et al. 2017). For tropical/subtropical areas, this warming poses a distinct risk to many species since many will already be near their thermal optimum or thermal maximum (Deutsch et al. 2008; Araújo et al. 2013). Furthermore, Puerto Rico lies within an area that is consistently projected to experience drier conditions as the climate warms. This “subtropical drying” is in contrast to the expected global (average) response to warming, where wetter conditions are predicted as a direct consequence of the fact that a warmer atmosphere will contain more water vapor (He and Soden 2016; Wuebbles et al. 2017). The possibility that Puerto Rico could experience a warmer and drier climate in the future poses significant risks to the water supply (Van Beusekom et al. 2016) and to the integrity of the mesic ecosystems that dominate the Arecibo watershed (Henareh Khalyani et al. 2016).

**Land Use Patterns and Change** Puerto Rico harbors a high human population density (438/km<sup>2</sup>), with 52% of its area classified as urban (16%) or densely populated rural (36%; Martinuzzi et al. 2007). Densely populated rural areas are perhaps the most pertinent urban class from a conservation perspective because it results in a high level of landscape fragmentation and habitat degradation. Urban and densely populated rural areas are present in the Rio Grande de Arecibo watershed, but are particularly prevalent in the eastern portions of the coastal wetlands between Arecibo and

Sabana Seca (Martinuzzi et al. 2007). The region also contains prime farmland suitable for mechanized agriculture (Gould et al. 2017). There is pressure to revamp the local economy through new development that converts permeable to impervious surfaces. However, with a recently declining human population on the island, the possibility of revamping existing infrastructure might be emphasized without encroaching on permeable lands (Gould et al. 2017).

**Ecological Basis for Vulnerability in Amphibians** The abundance and distribution of *Eleutherodactylus* frogs is strongly influenced by the availability of narrow microclimatic conditions to facilitate skin-mediated oxygen and ionic exchange and maintain metabolic rates (Joglar 1998; Barker and Rios-Franceschi 2014). Occupancy probability and abundance of various species of *Eleutherodactylus* are associated with precipitation and temperature gradients (Campos-Cerqueira and Aide 2017; Monroe et al. 2017a). Warmer and drier trends have triggered local extirpations of 2 species (*E. eneidae* and *E. karlschmidti*) at lower elevations at El Yunque National Forest (Campos-Cerqueira and Aide 2017). However, known minimum and maximum tolerance limits have been reported only for *E. coqui* (7.2–37.2 °C) and *E. portoricensis* (7.5–36.3 °C; Christian and Nunez 1988). Warming trends have also been implicated with higher mortality and reproductive failure of coquis (Burrowes et al. 2004, 2008). Species in this group exhibit direct-development. Thus, resiliency is greatly enabled by their ability to engage in positive niche tracking if suitable locations are connected (Barker and Rios-Franceschi 2014, Monroe et al. 2017b). Coastal populations of amphibians face the prospect of increasing salinity (Hopkins and Brodie Jr 2015; Albecker and McCoy 2017). Rios-López (2008) showed that abundance of adults of *Leptodactylus albilabris* decreased with increasing salinity, and reported a reduction in the number of larvae surviving to metamorphosis at salinities of 8 ppt. Admittedly, the vulnerability of *Leptodactylus albilabris* might be greater than for *Eleutherodactylus* frogs because the former has a tadpole stage. This does not preclude the possibility that oviposition sites for species like *E. juanriveroi* will be vulnerable (Albecker and McCoy 2017). The potential for local adaptations raises the need to better understand genetic variation and population structure. Our understanding for *Eleutherodactylus* frogs is poor with the exception of *E. coqui* (Velo-Anton et al. 2007) and *E. antillensis* (Barker and Rodríguez-Robles 2017). This understanding is needed to protect genetic representation of populations exhibiting potential adaptations to environmental changes.

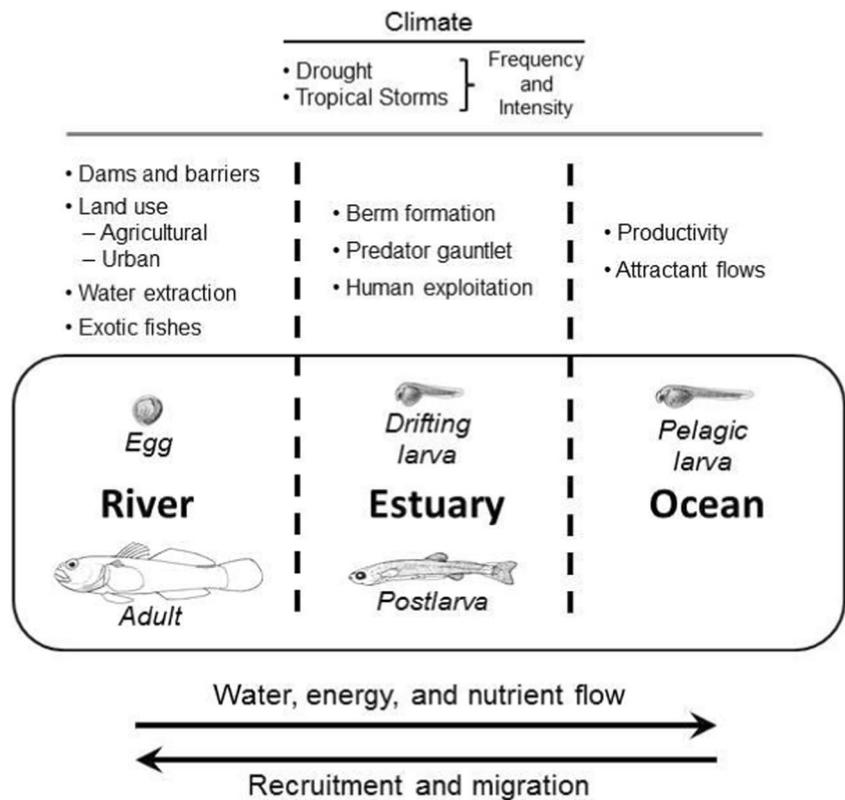
#### Ecological Basis for Vulnerability in Amphidromous Fishes

The successful downstream transport of Sirajo Goby larvae to the ocean and return migrations of postlarvae and juveniles to adult habitats in freshwater streams (recruitment) are

essential to the amphidromous life history (Fig. 3). The spawning and recruitment phenology of Sirajo Goby appears to enhance larval survival and postlarval recruitment success, but also makes this taxon sensitive to flow regime alterations. Sirajo Goby spawning is temporally concentrated so that downstream transport of larvae and upstream postlarval recruitment occur during periods of relatively high mean daily rainfall (i.e., high river discharge). Sirajo Goby gonadosomatic index increases sharply in April and May when river discharge begins to increase and decreases in early December, a time approximately equal to one mean pelagic larval duration (59 days) before the beginning of the dry season (Smith 2012; Engman et al. 2017b). High discharge during downstream transport of larvae presumably enhances survival by decreasing transport time to brackish or marine water, because sicydiine larvae survival and development in freshwater sharply decreases 2–4 days after hatching (Bell and Brown 1995; Iida et al. 2010). Reduced river discharge due to drying or water extraction would reduce the probability of successful downstream larval transport or increase transport time that could cause physiological stress and increased larval mortality. Water withdrawal facilities also cause mortality by entraining larval organisms (March et al. 1998). River discharge is also critical to Sirajo Goby recruitment success, which is synonymous with cetí abundance for the fishery. Cetí abundance is positively related to river discharge, possibly because rheotactic or olfactory cues direct migration to river mouths (Engman et al. 2017b). Sirajo Goby recruitment in Puerto Rico principally occurs from June through January during several days of the last quarter moon phase days (20–28 of the lunar cycle). Reduced discharge during narrow-windowed recruitment opportunities (i.e., around the last quarter moon phase) would limit freshwater attractant flows and reduce wetted area of migratory corridors that may result in decreased postlarval abundances and fishing success. Furthermore, reduced recruitment could have negative effects on the entire island's population because recruitment is critical to the metapopulation dynamics of fishes with marine pelagic larval phases such as Sirajo Goby (Caley et al. 1996).

In Puerto Rico, on-shore wave action builds sand berms, which during some low flow periods restrict or completely block river mouths, effectively closing the migration pathway for larval and postlarval amphidromous fishes (Negrón-Gonzalez and Cintrón 1979). Freshwater spates remove sand berms and occur frequently during the rainy season of non-drought years. However, water capture by reservoirs combined with reduced precipitation and river discharge would reduce the frequency and intensity of spates and increase the probability of recruitment failure due to connectivity loss. There are at least 335 artificial barriers to amphidromous fish migration (i.e., dams and other instream structures) that reduce or eliminate essential river connectivity in Puerto Rico streams and rivers (Cooney and Kwak 2013; Engman et al. 2017a).

**Fig. 3** Life history of Sirajo Goby, including life stage-specific threats and drivers of population dynamics (bullet points). Arrows indicate upstream and downstream movements



### Problem Structure and Decision Models

An integrated strategy, by definition, is a plan of action intended to accomplish multiple objectives. At landscape levels, problems will become multidimensional, as spatial and temporal complexity increases, requiring unique analytical approaches to identify solutions (Laber et al. 2018). We illustrate a possible pathway toward integrative decisions by identifying and categorizing elements or steps that constitute the framework of a strategy (Table 1). This process is most effective and complete when stakeholders work in conjunction with decision analysts. Our intent was not to render an exhaustive list of objectives and actions, but to highlight several that would likely be included in such a strategy. For the purpose of this illustration, we draw the attention of the reader to hydro-management as it is pertinent to conservation of water resources, but at the same impinges on self-sustaining populations and risks of extinction of the two taxonomic groups of interest (Table 1). Hydro-management serves both as a means objective (how to attain the fundamental objective) and action(s) that span the life cycles of both taxonomic groups and influence the degree of water resource benefits for humans. We also list measurable attributes or consequences that might stem from actions, sources of uncertainty, and potential topics that represent areas where trade-offs need to be assessed. Other opportunities for integrated models and

decisions might be identifiable by constructing influence diagrams (Runge 2011), helping to bear out key interdependencies that stem from actions in Table 1.

We constructed a numerical and conceptual (intuitive) decision model that represent real-world conditions where decision makers must assess the potential consequences of choosing an action or set of actions given the multiple (and possibly competing) objectives outlined in the problem framing step (Fig. 1). The two models reflect the heterogeneous nature of the wetlands landscape, but still illustrate the integration of human and conservation objectives using a common thread—water resources. The complexity and resolution of each model was driven by our understanding of species requirements for survival, threats or factors that impinge on them, and hypothetical variables and parameters involved in the decision.

### Plains Coqui - Aquifer Management Model

To address the conservation of water resources and amphibian-related objectives, we use a numerical decision model that maximizes human and conservation benefits in an environment whose quality could be threatened by anthropogenic salinization (Anderson 1976; Torres-González and Diaz 1984; Olcott 1999). Decisions involved balancing withdrawals of freshwater to maintain habitat quality for the plains

**Table 1** Elements of a structured decision making framework to address water and biological resource adaptive conservation in the Rio Grande de Atrecibo watershed and wetlands

Resource of Interest	Water	Amphibians	Amphidromous Fish
Objective	Sustainable Use Maximize quantity and quality	Sustainable Population minimize risk of extinction	minimize risk of extinction Sustainable Fishery
Means	Essential Habitat, Climatic Refuges Population Interventions, Watershed Integrity, Hydro-Management, Harvest Regulations, Partnerships		
Actions	Management in-situ and off sites - hydro-management, expand forest/wetland reserves, shade restoration, dam removal, harvest limits, regulate treatment plant outflow, create climate refuges, Translocate/supplement		
Consequences	Local Survival, recruitment, harvest landings, water quantity, quality, range shifts		
Trade-offs Assessments (when, where and how?)	Timing and magnitude of hydro-management, dam removal, harvest quotas, translocations/supplementations, costs		
Key Uncertainties	Climate Projections Threats (Land Use, Urban Growth) Hydro-management Catastrophic/Severe Events		

coqui (conservation benefit), but at the same time meeting human needs without exacerbating salt intrusion (human benefits). For the purpose of our example, we assumed that hydro-management of the unconfined aquifer in the area was essential to maintain environmental conditions within suitable bounds for the plains coqui.

Our aquifer management model can be described by the variables, parameters and functional relationships summarized in Table 2. The model is driven by the dynamics of two variables, the height of the current water table,  $T$ , and the salt (brackish) water level ( $B$ ); these levels are normalized so  $B \leq T \leq 1$  and  $B \leq s \leq 1$ , where  $s$  is the current sea level. The current amount of fresh water ( $F$ ) is the distance  $T - B$  between the water table and the salt water level. The manager chooses a desired withdrawal level  $A$ , but the actual withdrawal  $W$  is the desired withdrawal unless it exceeds the amount of fresh water plus the recharge ( $R$ ). The amount of fresh water after recharge and withdrawal is the current fresh plus recharge less withdrawal unless this is above the maximum amount of fresh possible, which is  $1 - B$ .

The actual amount withdrawn (after recharge) is given by

$$W = \min(A, \min(1 - B, T - B + R))$$

This implies that the fresh water remaining after withdrawal

$$F = \max(0, \min(1 - B, T - B + R - W))$$

The salt water level in the next period depends on the amount of fresh water  $F$  but never exceeds the sea level  $s$ :

$$B^+ = B + \theta \max(0, 1 - F) \frac{\max(0, s - B)}{s}$$

The impact of the current salt water level and the post recharge and withdrawal amount of fresh water on the future salt water level is shown in the right panel of Fig. 4. Notice that this implies that sea water level increases are irreversible:  $B^+ \geq B$ , a simplifying assumption in our model. The model is completed with the level for the next period water table:

$$T^+ = \min(1, B^+ + F^+)$$

In light of uncertainty regarding projected precipitation, we arbitrarily specified that rainfall would be capable of recharging 10% of aquifer annually; recharge is assumed to be described by a Beta distribution (Fig. 4, left panel).

The utility function is composed of two parts. The first is the utility of the withdrawals for human consumption and uses:  $U_h(W)$ . The second is the conservation benefits that arise due to the level of the water table and the amount of fresh water which, in combination, support the quality of fresh

**Table 2** Variables, parameters, and functional relationships for an aquifer under the hypothetical decision model to manage water in the Sabana Seca freshwater wetlands, Puerto Rico

Variables:

$T$ : water table level measures the height of the water in the aquifer (state)

$B$ : salt water level  $S \in [0, 1]$  measures the fraction of the aquifer that is brackish (state)

$F$ : amount of fresh water

$R$ : recharge i.i.d. w/ probability  $\pi$

$A$ : desired withdrawal for human consumption (action)

$W$ : actual withdrawal

Parameters:

$s$ : sea level, the maximum level of  $B$

$\alpha, \beta$ : parameters of the recharge probability:  $R \sim \text{Beta}(\alpha, \beta)$

$\theta$ : parameter governing the salt water level increase

$c, q$ : parameters governing the conservation benefits function

$\delta$ : discount factor

Functional relationships

$$F = T - B$$

$$W = \min(A, \min(1 - B, F + R))$$

$$F^+ = \max(0, \min(1 - B, F + R) - W)$$

$$B^+ = B + \theta(1 - F^+)(s - B)/s$$

$$T^+ = \min(1, F^+ + B^+)$$

$$U_h = W$$

$$U_c = \frac{F}{1 + e^{-q(T-c)}}$$

$$U = U_h^{1-\lambda} U_c^\lambda$$

water wetlands. Specifically  $U_c(B, T) = \frac{T-B}{1+e^{-q(T-c)}}$ . The total utility is given by the product  $U = U_h^{1-\lambda} U_c^\lambda$  where  $\lambda \in [0, 1]$ ; increases in  $\lambda$  put more relative weight on conservation benefits.  $U_c$  and the total utility for 2 values of  $\lambda$  are shown in Fig. 5. Future utility values are discounted using a discount factor of  $\delta = 0.98$ ; this relatively high discount factor indicates that we value the future substantially, consistent with our

fundamental objective. The optimal action is obtained by solving the Bellman equation

$$V(B, T) = \max_{0 \leq A \leq 1-B} E_R \left[ U_h(W)^{1-\lambda} U_c(B, T)^\lambda + \delta V(B^+, T^+) \right]$$

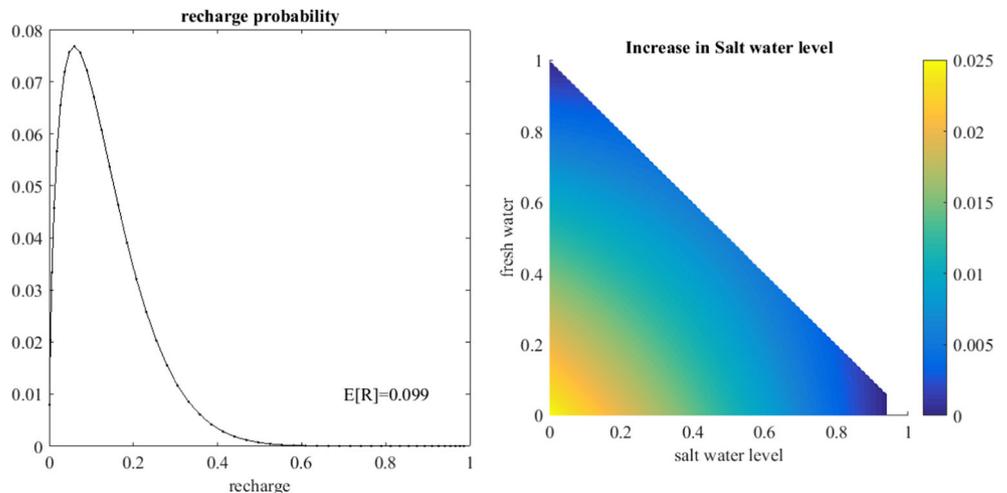
With this model we created two scenarios. First, suppose we set with  $\lambda = 0.5$  which puts equal weight on the human consumption and conservation benefits. In the second scenario, we placed higher weight on the conservation value of the aquifer for frogs ( $\lambda = 0.75$ ), a possibility that might be advanced by some stakeholders because there is only one known extant population of plains coqui. The strategies associated with the two  $\lambda$  values are shown in Fig. 6.

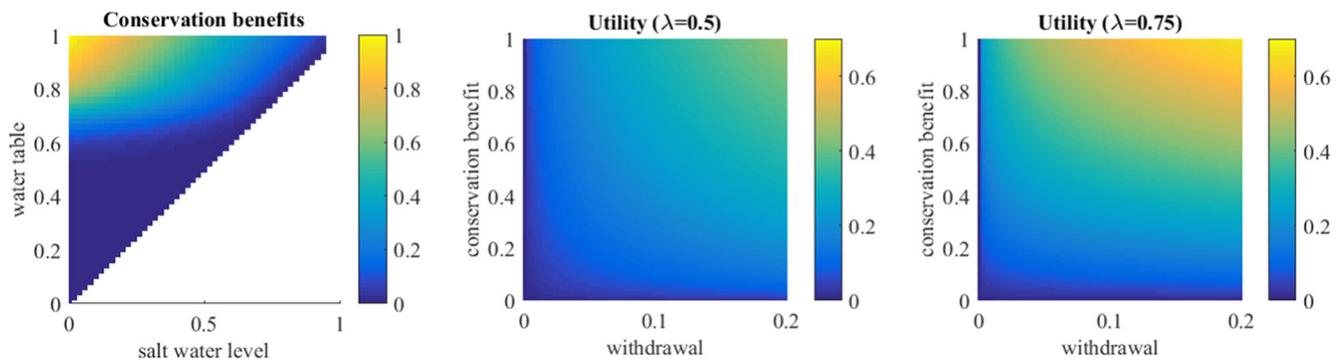
The action outcome for a utility with  $\lambda = 0.5$  shows that the optimal withdraw is to stop withdrawing water for human uses if the water table drops below 0.65 (darkest blue, left panel). Fig. 7 shows expected paths of the salt water level, water table and withdrawals over 200 year starting with  $B = 0$  and  $T = 1$ . In both panels the table decreases initially (with withdrawal of water), and the amount of salt intrusion (brackish) increases steadily over the whole period. When conservation is more highly valued ( $\lambda = 0.75$ ), however, the water table is maintained at a higher level and the salt water level rises at a slower rate. The model suggests that reducing water withdraws now (i.e., managing toward higher water tables for conservation) will delay salt intrusion, which in turn, will allow for a longer period of sustainable freshwater withdraws for people.

**Sirajo Goby – Hydroelectric Dam Model**

We envision a simpler conceptual (intuitive) decision model that balances conservation (Sirajo Goby spawning and recruitment success) and human (hydroelectric power, consumptive water use, cetí availability) needs based on the water levels at the Dos Bocas Dam, and at the USGS gaging station

**Fig. 4** Annual recharge probability (10%) of a hypothetical unconfined aquifer following a Beta distribution, and the impact of the current salt water level, post recharge and withdrawal amount of fresh water on the future salt water level





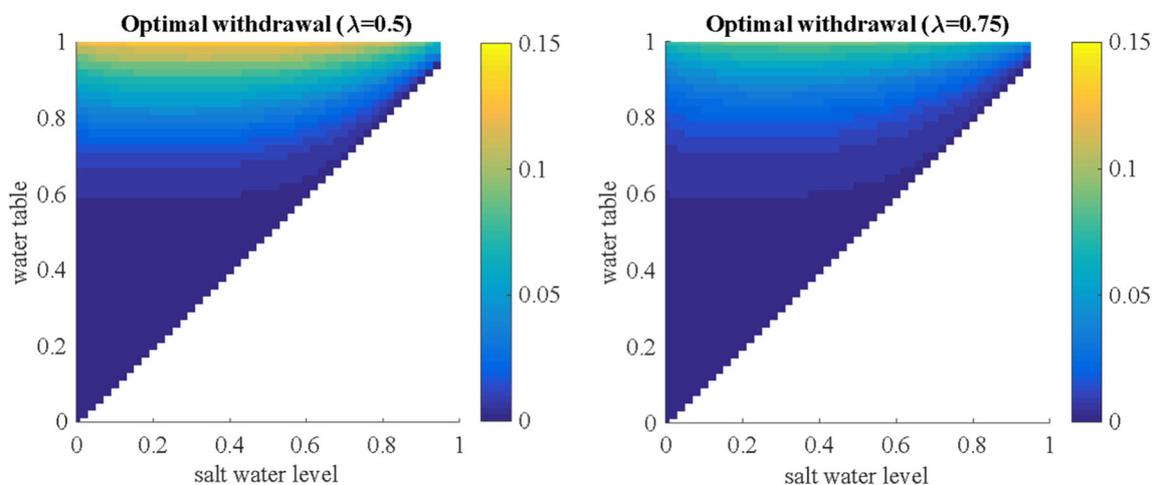
**Fig. 5** Total utility functions with alternative values of  $\lambda$ . One value of  $\lambda$  puts more relative weight on conservation benefits ( $U_c$ ) than on human consumption ( $U_h$ )

5,002,900 on the main stem Río Grande de Arecibo. The model needs to account for the annual reproductive cycle of Sirajo Goby (e.g., river spawning and downstream larval transport to the ocean), which primarily occurs from May through November, and post-larval recruitment (movement into and up river), primarily during the days of the last quarter moon phase from June through January (Smith 2012; Engman et al. 2017b). This annual reproductive cycle brackets the Puerto Rico rainy season; highest mean daily rainfall amounts occur between August and November while January through March are particularly dry months.

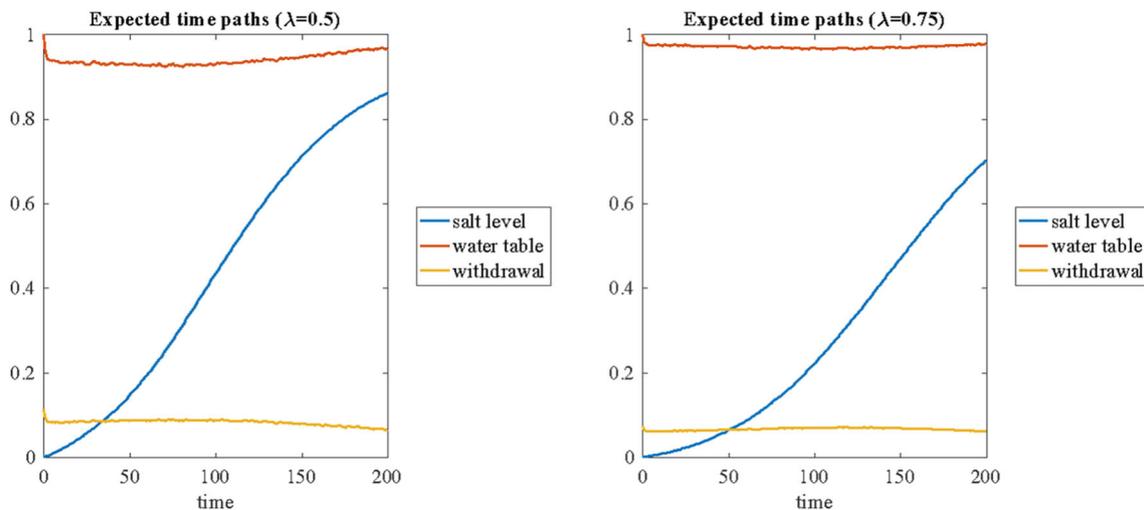
Decisions entail determining when water flows can be released from the dam while maintaining water storage at acceptable levels for hydroelectric power generation or consumptive uses. We would consider acceptable levels in the Dos Bocas reservoir to be the volume of water between the reservoir’s maximum capacity and minimum level required to produce hydro-power. Although detailed hydrological modeling and habitat-flow relationships would be required to properly quantify instream flows in terms of their timing, frequency, magnitude (volume/unit time), duration, and rate of change (Poff et al. 1997), we describe three conceptual instream flow types that may benefit Sirajo Goby conservation: (1) berm-

breaching spates, (2) spawning and river mouth maintenance flows, and (3) attractant flows for post-larval recruitment. Flow type 1 is a very high-magnitude but relatively low-duration flow that could be implemented as needed, based on observed or modeled river mouth conditions. Flow type 2 may be a minimum flow rate or range of flows to be maintained through spawning and recruitment seasons to ensure adequate available spawning habitat in the river, successful downstream transport of larvae, and to prevent the initiation of the formation of a berm at the river mouth. Flow type 3 would describe flows of intermediate duration that occur during the last-quarter moon phase, from June through January, at magnitudes that maximize recruit abundances.

We created a decision tree to illustrate how hydrological modeling and seasonal rainfall patterns may influence river-regulation decisions to optimize production of hydroelectric power and goby population persistence in the Rio Grande de Arecibo watershed (Fig. 8-top panel). The first level of decision is to determine whether water will be released or not. If the answer is “no”, then there is a higher risk of local goby extirpation. If the answer is “yes”, then there are several choices influenced by the hydrodynamics of the reservoir and the biology of goby. The simplest decision comes if



**Fig. 6** Optimal desired withdrawals of freshwater from a hypothetical unconfined aquifer with alternative values of  $\lambda$  (0.50 and 0.75)

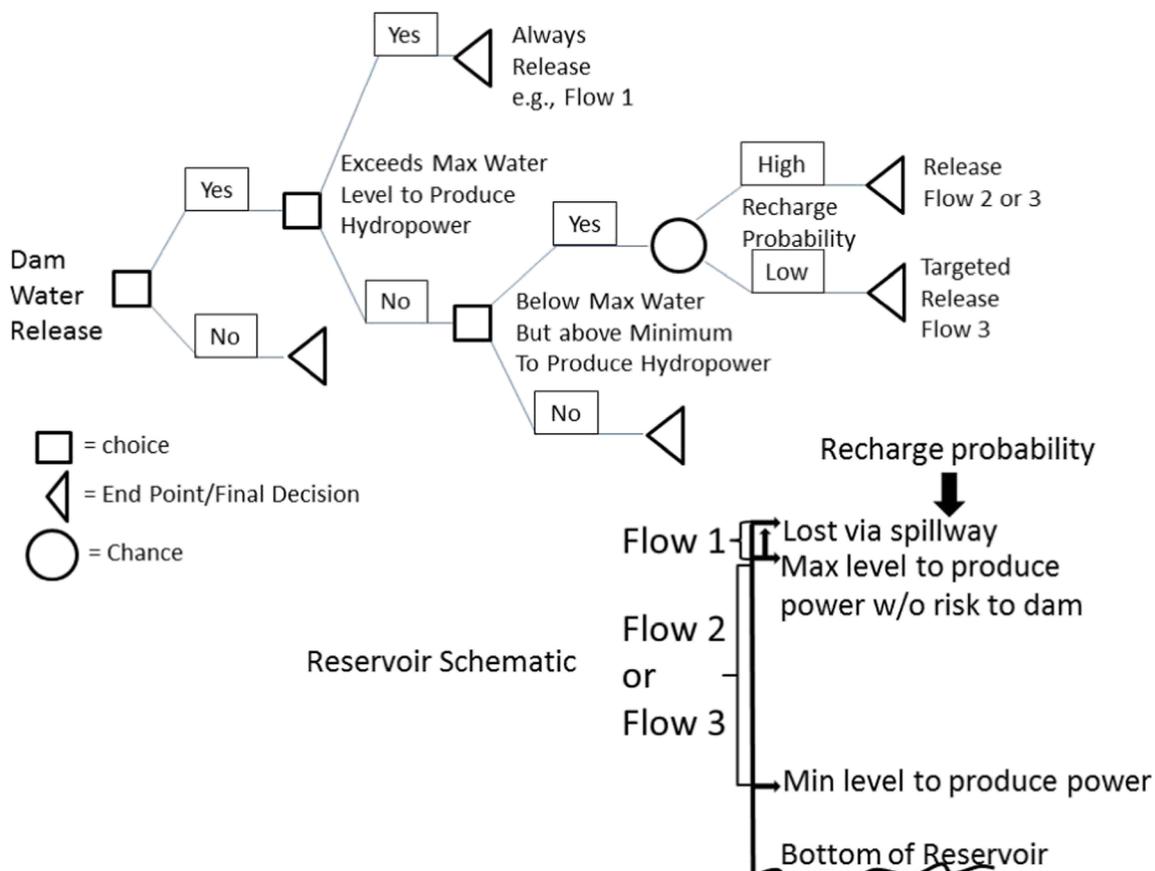


**Fig. 7** Expected time paths of salt water level, water table and withdrawals with optimal management over 200 years. The water table decreases initially (with withdrawal of water), and the amount of salt

intrusion (brackish) increases steadily ( $\lambda=0.50$ ), except when conservation is more highly valued ( $\lambda=0.75$ ). Then, the water table is maintained at a higher level and the salt water level rises at a slower rate

reservoir water levels exceed the maximum required to produce hydroelectric power. In that range of water levels, water flows out of the reservoir via spillway or could be released in greater pulses (volume) to breach sand berms downstream

without negative consequence to hydropower production and other consumptive uses (Fig. 8-bottom panel). These circumstances are more likely to take place during the peak of the rainy season (i.e., August through November). The frequency



**Fig. 8** Decision tree depicting decisions and conditions that could influence the type of water flow that will be selected to benefit both human consumption (e.g., hydroelectric power) and goby fish

persistence in the Rio Grande de Arecibo watershed. We also include a conceptual schematic of the Dos Bocas Reservoir highlighting water level thresholds that drive the decision-making process

of releases (pulses) daily, as needed, but they would be of short duration (i.e., less than a day). During this period, releasing water under flow scenarios 2 and 3 is also possible provided water levels are within the maximum and minimum levels to produce hydropower and there is a high probability of reservoir recharge (e.g., non-drought years, Fig. 8). Under these scenarios, water releases could mimic the natural flow regime of the Río Grande de Arecibo as closely as possible without depleting reservoir water levels below acceptable levels. However, if the probability of reservoir recharge is lower (e.g., lower precipitation probability, drought, higher demand for water for human use, Fig. 8), then releases would take place only as needed. For example, during the postlarval recruitment season (June–January), water could be withheld during periods outside of the last quarter moon phase to store water and raise the reservoir level. Water would be released at the 3rd quarter moon phase (days 20–28 of the lunar cycle) with attractant flows released as available before the recruitment period, while maintaining type 2 flows in the river. Type 2 flows may be released to facilitate transport of larvae to the river mouth and estuary during the months of May through November. In all scenarios, a minimum water release would be required to sustain aquatic biota in the downstream, non-tidal river reach.

### Integrate Planning, Decision Analysis and Monitoring

Given the vulnerabilities and uncertainties impinging upon the aforementioned decision contexts, implementation of an agreed-upon strategy should give high priority to feasible adaptive actions, or those that have a chance of succeeding. One such option was captured and illustrated by our first decision model. It focused on in-situ actions aimed at maintaining habitat within a range of suitable conditions through the management of the state of an unconfined aquifer. As shown, consequences were predicated on how much weight was placed on human versus conservation benefits from water resources. Clearly, our aquifer model was an oversimplification of a salt intrusion hydro-dynamic model (see Verruijt 1968). Nonetheless, our exercise draws attention to salt intrusion as a potential environmental forcing for some coastal wetlands in Puerto Rico and the trade-offs between withdrawing higher volume of freshwater at present versus a reduced amount over a longer term (Anderson 1976; Torres-González and Díaz 1984; Olcott 1999). Increasing salinity is already affecting demographic parameters of forested wetlands comprised of *Pterocarpus officinalis* in portions of the freshwater coastal wetlands harboring the plains coqui (Rivera-Ocasio and Aide 2007). Continued salt intrusion could favor euryhaline plant and animal communities adapted to brackish

conditions (Rios-López 2008), communities that are also highly productive and valued by the ecological services they provide (Kelleway et al. 2017).

We note that not all decisions and actions on the landscape require complex models. Many can be intuitive, but need to be well informed and detailed as necessary as we illustrated with the Sirajo Goby. Other intuitive actions include maintaining forest cover or expanding existing reserves in the upper reaches of the watershed. Such actions would help maintain micro-climatic conditions required by other species of *Eleutherodactylus* (Monroe et al. 2017a), and protect the headwaters of the Río Grande de Arecibo. Among the portfolio of actions is also the opportunity to use agroecosystem practices to help preserve watershed integrity and biological resources (Monroe et al. 2017b; Perfecto and Vandermeer 2015; Irizarry et al. 2018).

### Discussion

Arguably, the Anthropocene has led to a global setting where ecological and human dynamics are intertwined (Lui et al. 2007; Kareiva and Marvier 2012). Depending on the resource of interest, the Anthropocene raises concerns about the persistence of many elements of biological diversity (e.g., Urban 2015; Irizarry et al. 2016), but in some instances, it also presents opportunities to integrate human activities and conservation (e.g., Radeloff et al. 2015; Irizarry et al. 2018). We recognize that formulating a strategy in this context needs to be robust and adaptive in terms of the incremental actions taken over time, but also in terms of the evolving nature of societal values, and varying perceptions and tolerance to risks and uncertainty from various sectors of society (Wise et al. 2014). Our illustrative strategy began by highlighting the rationale for selecting the watershed-wetlands complex. It also underscored water as a resource of mutual benefit for humans and biological resources.

We chose resiliency as the driving ecological principle behind the strategy as it permits decision makers to opt for natural recovery/regeneration of resources in the advent of environmental change, or engage in pro-active management or assisted recovery (Nichols and Williams 2006; Heller and Zavaleta 2009; McDonald-Madden et al. 2011; Falk 2017; Matzek et al. 2017). To illustrate this facet of the problem framing and planning phase, we specified that the fundamental objectives of the strategy were to maximize the probability of self-sustaining use of water resources and conservation of populations of plains coqui and Sirajo Goby. Implicitly, the fundamental objectives valued the importance of sustaining a fishery and water resources for human consumption, and the prominent role played by *Eleutherodactylus* frogs and Sirajo Goby in energy flow of ecosystems in Puerto Rico.

In our estimation, the question of interest for decision makers is how to stay within an adaptive, resilient space over time? We highlight two aspects of scientific knowledge required to achieve this objective. The first is that decisions will be best informed by an understanding of how individuals or populations respond to disturbances; specifically, knowledge about population and genetic adaptations to variable environments, dispersal and migration strategies to track changing environmental conditions (Wang et al. 2010; Tingley et al. 2014; Falk 2017). We showed that a review of foundational research and knowledge can provide valuable insights to construct initial but appropriate decision models. For example, recent foundational, seminal research has shown that the Sirajo Goby's amphidromous life history requires river-ocean connectivity and adequate river flow to complete early life-stage migrations (Kwak et al. 2016). Initial models could be followed by an adaptive process (recurrent decisions) whereby knowledge about ecological dynamics is accrued by discriminating among competing models of system response to management (Nichols and Williams 2006).

The second aspect is accounting for uncertainty associated with major environmental factors, and how to incorporate it into decision models. It is important to evaluate the 'uncertainty context' before decision modeling is undertaken. Under conditions of uncertainty, robust decision making or a precautionary approach are likely to be more appropriate and useful (Weaver et al. 2013). Efforts to reduce uncertainty, such as targeted and long-term surveillance monitoring programs (Wintle et al. 2010), will be an important to facilitate learning.

As an example, in our decision models, a significant source of uncertainty is the probability of water recharge of aquifers or the reservoir (Henareh Khalyani et al. 2016; Van Beusekom et al. 2016). Recharge can have many pathways, but ultimately, it is primarily driven by rainfall (Torres-González and Díaz 1984). As such, projections of precipitation are crucial for assessing tradeoffs, and are also deeply uncertain. And yet, the science to support precipitation projections in Puerto Rico has evolved in just a few years. Hayhoe (2013) developed projections using a statistical relationship between local climate variables (temperature, precipitation) and global climate model (GCM) predictors. Prior to this, the only information available came from very coarse resolution GCMs that could not resolve the island relative to the surrounding ocean. This statistical downscaling effort was more recently followed by an effort to explicitly resolve the process-based physical dynamics of the regional climate system using higher resolution regional climate models, also known as dynamic downscaling (Wootten et al. 2016; Bhardwaj et al. 2018). It is hoped that continuing efforts on multiple approaches, such as this, will help characterize, quantify, and possibly even reduce uncertainty over time.

Attempts to quantify and account for uncertainty also apply to urban growth. For example, urban planning in Puerto Rico over the last 40 years has been deemed ineffective, resulting in

a substantial amount of high density rural areas (Martinuzzi et al. 2007). This type of development is considered a major contributor of habitat fragmentation, and it has occurred primarily on lands of value for other uses (e.g., agriculture; Gould et al. 2017). Uncertainty is exacerbated because while the island has undergone an economic downturn and loss of human population over the last 10–15 years, population numbers in rural areas continue to expand, many in the vicinity of protected areas (Castro-Prieto et al. 2017). In our illustrative landscape, urban sprawl is considered a major threat to wetland habitats (Rios-López 2008; Martinuzzi et al. 2007). Thus, even under a scenario of no growth, development already poses formidable physical barriers to species like the plains coqui. This constraint limits the implementation of traditional adaptation strategies like expanding protected areas or connecting disjoint suitable habitats (Heller and Zavaleta 2009).

In this work, we highlight various components necessary to frame a resilience-based conservation strategy, and although it was not the focus of the paper, we cannot overemphasize the importance of incorporating benefits and adjusting the strategy as human values and priorities evolve (Wise et al. 2014). While we focused on the biological values of the Sirajo Goby and plains coqui, and the value of water resources for multiple uses, we also recognize that it is essential to identify essential stakeholders during the framing process. For example, Caño Tiburones is managed by three governmental agencies with potentially competing objectives (e.g., wildlife protection and recreation vs. agricultural irrigation). We encourage planners and decision makers to explore path dependencies among actions, societal values and needs, present and future, to increase the likelihood of a successful conservation strategy.

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