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Modeling the impacts of global warming on predation and biotic resistance: mosquitoes, damselflies and avian malaria in Hawaii

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Abstract Biotic resistance from native predators can play an important role in regulating or limiting exotic prey. We investigate how global warming potentially alters the strength and spatial extent of these predator–prey interactions in aquatic insect ecosystems. As a simple model system, we use rock pools in streams of rainforests of Hawaii, which contain the beautiful Hawaiian damselfly *Megalagrion calliphya* as predator and the invasive southern house mosquito *Culex quinquefasciatus* as prey. This abundant mosquito is the major vector of avian malaria transmission to native forest birds. We use mathematical modeling to evaluate the potential impacts of damselfly predation and temperature on mosquito population dynamics. We model this predator–prey system along an elevational gradient (749-1952 m elevation) and assess the effect of 1°C and 2°C climate warming scenarios as well as the effects of El Niño and La Niña oscillations, on predator–prey dynamics. Our results indicate that the strength of biotic resistance of native predators on invasive prey may decrease with increasing temperature because demographic rates of predator and prey are differentially affected by temperature. Future warming could therefore increase the abundance of invasive species by releasing them from predation pressure. If the invasive species is a disease vector, these shifts could increase the impact of disease on both humans and wildlife.

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Introduction

Human-mediated biological invasions are important drivers of global ecological changes which may reduce the diversity of native species and threaten the functioning of ecosystems (Mack et al. 2000). When the invasive species is a disease vector, this may also have significant consequences for disease transmission in wildlife, domestic animal, and human systems (Harvell et al. 2002). Prevention, management, or eradication of biological invasions is therefore important and requires knowledge of the factors that influence the outcome of an invasion process.

An invasion process can be divided into introduction, colonization, establishment, and spread phases (Walther et al. 2009). Whether a species will advance through all these phases and become a successful invader depends on the

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(combination of) propagule supply, attributes of the species, abiotic conditions, and the strength of biotic resistance of the native community to an introduced species (Mack et al. 2000). "Biotic resistance" can be defined as the interactions of the native species in a community with non-native species that exclude or slow the growth of those non-native species (Cain et al. 2011). Suggested mechanisms of biotic resistance are predation, competition, pathogens, parasites, and a lack of suitable mutualists (Elton 1958).

Native predators may significantly reduce the abundance of non-indigenous species (deRivera et al. 2005; Gruner 2005; Carlsson et al. 2009; Carlsson et al. 2011) or completely prevent its establishment (Dumont et al. 2011). The strength of predator–prey interactions is likely to change due to global warming (especially in poikilothermic systems), because higher temperatures may (1) increase the activity, searching rate, and prey handling time of predators and therefore prey consumption (Logan et al. 2006; Thompson 1978; Corbet 1999); (2) change the preference of a predator for prey species (Veiga et al. 2011); (3) result in mistiming between the presence of the predator and its food sources (Visser and Both 2005); (4) change the growth rates of both the predator and prey (Savage et al. 2004); and (5) indirectly affect the abundance of the predator by changing interactions with other species in the community (Montoya and Raffaelli 2010). Surprisingly however, studies on the effect of temperature on predator–prey dynamics at the population level are limited (Logan et al. 2006; Tylianakis 2009).

In this study, we explore the hypothesis that effects of global warming on predator–prey dynamics may also change the strength of biotic resistance of native predators to invasive prey species and therefore change the abundance and spatial distribution of the invasive species. For this purpose, we developed a mathematical model that describes the effect of temperature on the predator–prey interactions in a relatively simple aquatic insect ecosystem along an elevational gradient. This system consists of rock pools in streams in rainforests on the Island of Hawaii. The main predators in these pools are larvae of the native damselfly *Megalagrion calliphya* and their most abundant prey is the introduced southern house mosquito *Culex quinquefasciatus*. This mosquito is the vector of avian malaria (*Plasmodium relictum*), which is considered to be a primary factor contributing to population declines and changes in the geographic and elevational distribution of native Hawaiian forest birds (van Riper et al. 1986; van Riper 1991), especially Hawaiian honeycreepers (Drepanidinae; Jacobi and Atkinson 1995; Atkinson et al. 1995; Woodworth et al. 2005; Samuel et al. 2011). We discuss the potential effect of changes in biotic resistance to this invasive mosquito on the impact of avian malaria on Hawaiian honeycreepers.

Materials and methods

Model system

The Pahala watershed covers an elevational range of 700–2,000 m in the forest zone on the southern portion of the island of Hawaii (Fig. 1). Rock pools along montane rainforest streams in this area are frequently seep fed, creating a relatively permanent microhabitat, which is less prone to scouring than streams in lower parts of the Pahala watershed (R. Fontaine, personal communication). Aquatic systems on Pacific islands like Hawaii have a depauperate fauna (Benstead et al. 2009) and rock pools in upland streams are free from introduced fish or other major non-indigenous predators (DA LaPointe, unpublished data). In these pools, larvae of the damselfly *M. calliphya* are the top predators and larvae of the invasive mosquito *C. quinquefasciatus* are the most abundant prey (D. Foote, unpublished data).

Simulation model

We developed an ordinary differential equation model to describe damselfly and mosquito population dynamics and the predator–prey interaction between these two species (Eqs. 1–10). The life cycle of damselflies was divided into an egg stage (D_E), early (D_{LE}) and later (D_{LL}) larval instar stages, pre-reproductive (D_P) and reproductive (D_R) adult stages (Fig. 2). Early and later instar damselfly larvae were separated because only later instars, hereafter damselfly larvae, are large enough to prey on mosquito larvae. The
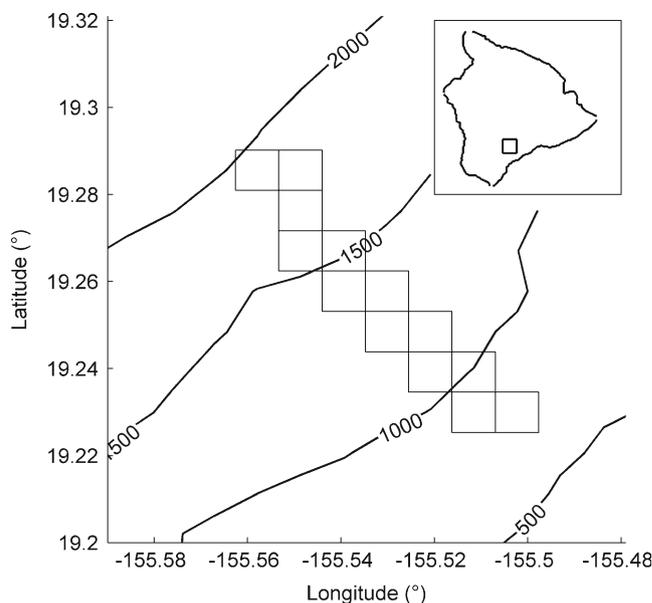

Fig. 1 The location of the grid cells for which the climate was calculated along an elevational gradient in the Pahala watershed on the island of Hawaii. Each grid cell represents an area of 1 km². Contour lines indicate elevation in meters

life cycle of *Culex* mosquitoes was divided into egg (M_E), larval (M_L), and reproductive adult (M_R) stages (Fig. 2). We model only one larval mosquito stage, because damselfly larvae feed on all larval instars of mosquitoes. A lag (or waiting) time is required for individual damselflies and mosquitoes to complete each developmental stage. However, in standard ordinary differential equation models, the probability to transit to the next developmental stage follows an exponential distribution where transit to the next stage is highest for individuals that just entered a stage. We used the "linear chain trick" (Anderson and Watson 1980; Feng et al. 2007; Lloyd 2001) to change the exponential distribution of development times to a gamma distribution, which has a similar shape as a positive Gaussian distribution for shape parameters (k) equal to or higher than 4–5. We set the value of the shape parameter to 5 to achieve reasonable waiting times for developmental stages, without overly increasing model complexity. State variables are expressed in number of individuals per liter of water in permanent rock pool habitat. For adult stages, this represents the number of individuals produced from 1 L of water in a rock pool.

The dynamics of all non-reproductive stages of damselflies and mosquitoes are determined by their recruitment rate, development rate (d_{stage}), and mortality rate (μ_{stage}) in the absence of predation. The dynamics of the reproductive stages are determined by their recruitment and mortality rates. We modeled the daily egg production for damselflies (Eq. 2a) and mosquitoes (Eq. 7a) (recruitment rate egg stages) as the product of the per capita egg production for a reproductive cycle (c), the fraction of adults that oviposite (g), and the number of adults. For all other stages, recruitment was determined by the development rate of the previous stage. We used density-dependent regulation of the first larval instars (Eqs. 3a and 8a) to prevent unlimited growth of the damselfly and mosquito populations.

Mosquito larvae are often the most abundant prey species of damselfly larvae in the depauperate rock pools of upland streams in Hawaii (D. Foote, personal communication). At low densities of mosquitoes, damselfly larvae may prey on other species (e.g., Chironomidae, see Williams 1936) to meet nutritional requirements, but they are assumed to switch to mosquito larvae as their only prey, when the density of mosquito larvae increases. This behavior of a predator is common among insects (Schenk and Bacher 2002) and the predation rate on the most abundant prey species can be modeled using a Holling type III functional response (Holling 1959), which leads to the following function for the predation rate (p) of damselfly larvae on mosquito larvae:

$$p(D_{LL}, M_L, T) = D_{LL}\left(\frac{sM_L^2}{1 + sh(T)M_L^2}\right). \tag{1}$$

In this equation, $h(T)$ is handling time as a function of temperature. The search time is proportional to prey density with proportionality constant s (Table 1). Predation on mosquito larvae substages (M_{Li}) was assumed to be proportional to the frequency of each substage in the total population of mosquito larvae ($p(D_{LL}, M_L, T)\frac{M_{Li}}{M_L}$). We assume that changes in the density of mosquito larvae do not significantly affect damselfly dynamics as they supplement their diet with other prey. In addition, adult damselflies are only active during the day and therefore not likely to prey on adult mosquitoes, which are most active at night (van Riper et al. 1986).

This leads to the following model equations for *M. calliphya* and *C. quinquefasciatus*:

Damselfly eggs

$$\frac{dD_{E1}}{dt} = c_D g_D D_R - \left(kd_{D_E}(T) + \mu_{D_E}\right)D_{E1}. \tag{2a}$$

$$\frac{dD_{Ei}}{dt} = kd_{D_E}(T)D_{E(i-1)} - \left(kd_{D_E}(T) + \mu_{D_E}\right)D_{Ei} \tag{2b}$$

$$D_E = D_{E1} + \sum_{i=2}^{i=k} D_{Ei}\ with\ i = 2, \ldots, k \tag{2c}$$

Damselflies

Reproductive adults

↑

Pre-reproductive adults

↑

Later instar larvae → *predation* → **Mosquitoes**

↑   (Alternative prey)

Early instar larvae

↑

Eggs

Mosquitoes

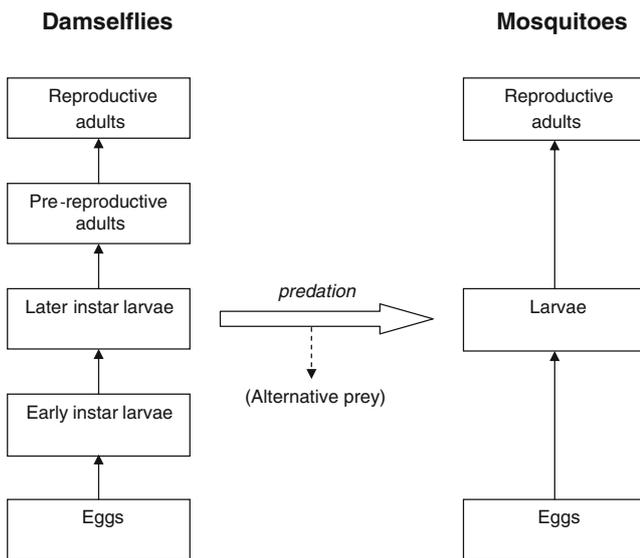Reproductive adults

↑

Larvae

↑

Eggs

Fig. 2 Simulation model structure for mosquito and damselfly development. Flows due to birth and mortality are not shown, but all individuals start as eggs. Later instar damselfly larvae may supplement their diet with alternative prey to meet nutritional requirements. The effect of the presence of alternative prey on the predation rate of mosquitoes is accounted for by using a Holling type III functional response. Although not shown in the figure, with the exception of the mature stages, all developmental stages were further divided into five substages to obtain gamma distributed sojourn times of individuals in developmental stages (see text)

Table 1 Abbreviations, descriptions, values, dimensions, and sources of the model parameters

Parameter	Description	Value	Dimension	Source
M. calliphya				
$1/d_{D_E}(T)$	Length of the egg stage	$\left(\frac{241}{T-11}\right)$	Day	1
$1/d_{D_{LE}}(T)$	Length of the early instar larval stage	$\left(\frac{\alpha 2883}{T-2.6}\right)$	Day	1
$1/d_{D_{LL}}(T)$	Length of the later instar larval stage	$\left(\frac{(1-\alpha)2883}{T-2.6}\right)$	Day	1
α	Fraction of the total larval stage that is spent as early instars	0.2	–	1
$1/d_{D_P}$	Length of the pre-reproductive adult stage	2	Day	1
μ_{D_E}	Mortality rate eggs	0.0129	Day^{-1}	1
$\mu_{D_{LE}}$	Mortality rate early instar larvae	0.0111	Day^{-1}	1
$\mu_{D_{LL}}$	Mortality rate later instar larvae	0.0120	Day^{-1}	1
μ_{D_P}	Mortality rate prereproductive adults	0.0875	Day^{-1}	2,3,4,5
$1/\mu_{D_R}$	Length of the reproductive adult stage	7	Day	1
c_D	Clutch size female eggs	70	–	1
l_D	Length reproductive cycle	2	Day	1
K_{D_L}	Maximum density larvae	5	Liter^{-1}	1
g_D	Fraction of the total number of reproductive adults that oviposits per day	$\left(\frac{\mu_{D_R}e^{-\mu_{D_R}l_D}}{1-e^{-\mu_{D_R}l_D}}\right)$	Day^{-1}	–
C. quinquefasciatus				
$1/d_{M_E}(T)$	Length of the egg stage	$\left(\frac{30}{T-10}\right)$	Day	6
$1/d_{M_L}(T)$	Length of the larval stage	$\left(\frac{149}{T-10}\right)$	Day	6
μ_{M_E}	Mortality rate eggs	0.108	Day^{-1}	7
μ_{M_L}	Mortality rate larvae	0.121	Day^{-1}	7
$1/\mu_{M_R}$	Length of the adult stage	13.9	Day	8
c_M	Clutch size female eggs	85	–	8
$l_M(T)$	Length reproductive cycle	$-2.25 + 241T^{-1.11}$	Day	8
K_{M_L}	Maximum density larvae	40	Liter^{-1}	1
$g_M(T)$	Fraction of the total number of reproductive adults that oviposits	$\left(\frac{\mu_{M_R}e^{-\mu_{M_R}l_M(T)}}{1-e^{-\mu_{M_R}l_M(T)}}\right)$	Day^{-1}	–
Functional response				
s	Proportionality constant for the searching rate and the prey density	0.0015	Liter^2/day	–
$h(T)$	Handling time of mosquitoes	$(0.0035T^2 - 0.19T + 3.1)h_{ref}$	Day	1
h_{ref}	Handing time of mosquitoes at 15 C	0.20	Day	1
Gamma distribution				
k	Shape parameter	5	–	–

1 D. Foote (unpublished data); *2* Cooper et al. (1996); *3* De Block and Stoks (2005); *4* Forbes and Leung (1995); *5* Hinnekint (1987); *6* Ahumada et al. (2004); *7* Hayes and Hsi (1975); *8* D.A. LaPointe (unpublished data)

Early instar damselfly larvae

$$\frac{dD_{LE1}}{dt} = kd_{D_E}(T)\left(1 - \frac{D_{LE} + D_{LL}}{K_{D_L}}\right)D_{Ek}$$
$$- \left(kd_{D_{LE}}(T) + \mu_{D_{LE}}\right)D_{LE1} \quad (3a)$$

$$D_{LE} = D_{LE1} + \sum_{i=2}^{i=k} D_{LEi} \text{ with } i = 2,\ldots,k \quad (3c)$$

Later instar damselfly larvae

$$\frac{dD_{LEi}}{dt} = kd_{D_{LE}}(T)D_{LE(i-1)} - \left(kd_{D_{LE}}(T) + \mu_{D_{LE}}\right)D_{LEi} \quad (3b)$$

$$\frac{dD_{LL1}}{dt} = kd_{D_{LE}}(T)D_{LEk} - \left(kd_{D_{LL}}(T) + \mu_{D_{LL}}\right)D_{LL1} \quad (4a)$$

$$\frac{dD_{LLi}}{dt} = kd_{D_{LL}}(T)D_{LL(i-1)} - \left(kd_{D_{LL}}(T) + \mu_{D_{LL}}\right)D_{LLi} \quad (4b)$$

$$D_{LL} = D_{LL1} + \sum_{i=2}^{i=k} D_{LLi} \ with \ i = 2,\ldots,k \quad (4c)$$

Pre-reproductive adult damselflies

$$\frac{dD_{P1}}{dt} = kd_{D_{LL}}(T)D_{LLk} - \left(kd_{D_P} + \mu_{D_P}\right)D_{P1} \quad (5a)$$

$$\frac{dD_{Pi}}{dt} = kd_{D_P}D_{P(i-1)} - \left(kd_{D_P} + \mu_{D_P}\right)D_{Pi} \quad (5b)$$

$$D_P = D_{P1} + \sum_{i=2}^{i=k} D_{Pi} \ with \ i = 2,\ldots,k \quad (5c)$$

Reproductive adult damselflies

$$\frac{dD_R}{dt} = kd_{D_P}D_{Pk} - \mu_{D_R}D_R \quad (6)$$

Mosquito eggs

$$\frac{dM_{E1}}{dt} = c_M g_M(T)M_R - \left(kd_{M_E}(T) + \mu_{M_E}\right)M_{E1} \quad (7a)$$

$$\frac{dM_{Ei}}{dt} = kd_{M_E}(T)M_{E(i-1)} - \left(kd_{M_E}(T) + \mu_{M_E}\right)M_{Ei} \quad (7b)$$

$$M_E = M_{E1} + \sum_{i=2}^{i=k} M_{Ei} \ with \ i = 2,\ldots,k \quad (7c)$$

Mosquito larvae

$$\frac{dM_{L1}}{dt} = kd_{M_E}(T)\left(1 - \frac{M_L}{K_{M_L}}\right)M_{Ek} \\
- \left(kd_{M_L}(T) + \mu_{M_L}\right)M_{L1} \\
- p(D_{LL}, M_L, T) \\
\times \frac{M_L1}{M_L} \quad (8a)$$

$$\frac{dM_{Li}}{dt} = kd_{M_L}(T)M_{L(i-1)} - \left(kd_{M_L}(T) + \mu_{M_L}\right)M_{Li} \\
- p(D_{LL}, M_L, T)\frac{M_{Li}}{M_L} \quad (8b)$$

$$M_L = M_{L1} + \sum_{i=2}^{i=k} M_{Li} \ with \ i = 2,\ldots,k \quad (8c)$$

Reproductive adult mosquitoes

$$\frac{dM_R}{dt} = kd_{M_L}M_{Lk} - \mu_{M_R}M_R \quad (9)$$

Parameter estimation

The definition, values, and dimension of model parameters are given in Table 1.

Parameters in M. calliphya model

With the exception of the mortality of pre-reproductive adults, all damselfly model parameters were estimated from field and experimental data (Table 1). We modeled the length of the egg ($1/d_{D_E}$) and larval stages ($1/d_{D_{LE}}$, $1/d_{D_{LL}}$) as a function of temperature according to the function (Trottier 1971)

$$1/d_{\text{stage}} = \frac{CD}{T - T_0}, \quad T > T_0 \quad (10)$$

where, CD is the number of degree days required to complete the developmental stage, T is the average daily temperature, and T_0 is the lower temperature threshold for development. There is no development at temperatures equal to and below this threshold temperature ($d_{stage}=0$). Parameters and were estimated by fitting Eq. 10 to experimental data on the length of the egg and larval stages in climate chambers at temperatures of 15°C, 22°C, and 28°C (D. Foote, unpublished data). The mortality rates of eggs (μ_{D_E}) and larvae ($\mu_{D_{LE}}$, $\mu_{D_{LL}}$) were calculated from the fraction of individuals that survived these stages at the temperatures above. The effect of temperature on mortality rates of immature damselflies was inconsistent and mortality rates were therefore assumed to be constant. The carrying capacity of *M. calliphya* larvae (K_{D_L}) was estimated from a survey of 10 rock pools during the summer of 2010 at the lower end of the elevational gradient in the forest of the Pahala watershed (D. Foote, unpublished data). These pools were assumed to be perennial, because they contained algae. Data on the effect of temperature on adult damselfly stages were not available. We estimated the mortality rate of pre-reproductive adult damselflies from the literature on damselfly species that do not use the pre-reproductive stage to bridge an adverse weather period, because environmental conditions in the tropical forest allow damselflies to develop and reproduce year round (at most elevations). In addition, only damselfly data from laboratory and outdoor insectary studies on females

were considered, so that background mortality rate was not influenced by predation (Cooper et al. 1996; De Block and Stoks 2005; Forbes and Leung 1995; Hinnekint 1987). We estimated the mortality rates of the reproductive adult stages as the inverse of their average longevity (Thieme 2003).

Parameters in C. quinquefasciatus model

The length of egg ($1/d_{M_E}$) and larval mosquito stages ($1/d_{M_L}$) were estimated from Eq. 10 using the cumulative degree days and threshold temperatures for these stages in Hawaii (Ahumada et al. 2004). Mortality rates of the egg and larval stage were derived from the fraction of individuals surviving these stages (Hayes and Hsi 1975). Daily temperatures along our elevational transect in the Pahala watershed were within tolerance ranges for *C. quinquefasciatus* (Ahumada et al. 2004; Hayes and Hsi 1975); therefore, we assumed that egg and larval mortality rates were constant (Ahumada et al. 2009). The carrying capacity of *C. quinquefasciatus* larvae was estimated from a survey of 14 rock pools in the Pahala watershed that were not inhabited by *M. calliphya* larvae at the lower end of the elevational gradient during the summer of 2010 (D. Foote, unpublished data). The length of the mosquito reproductive cycle was reduced for higher daily temperatures (Ahumada et al. 2009; Samuel et al. 2011).

Functional response

The searching rate and handling time ($h(T)$) of mosquito larvae by later instar damselfly larvae were estimated for a Holling type II functional response (Holling 1959) by fitting the random predator equation (Rogers 1972) to data on the consumption rate of second instar *C. quinquefasciatus* larvae by *M. calliphya* larvae in the absence of alternative prey (D. Foote, unpublished data). The random predator equation accounts for the effect of prey depletion on the searching rate and handling time (Rogers 1972). The experiment was conducted in environmental chambers at temperatures of 15°C, 22°C, and 28°C. At each temperature, the feeding rate of damselfly larvae was determined for prey densities of 20, 73, or 120 mosquito larvae per liter during a period of 3–4 days. The estimated handling time decreased with temperature. We modeled the dependence of the handling time on the temperature using a parabolic function (Table 1). This function for the handling time of a Holling type II functional response can also be used for a Holling type III functional response, because, in both cases, the handling time does not depend on the prey density. The value of parameter s in the Holling III functional response (Eq. 1) cannot be estimated using data from experiments with only prey species. In absence of data on the predation rate of mosquito larvae in the presence

of alternative prey, we estimated the value of this parameter by assuming that a Holling type II (parameters estimated from the experimental data described above) and Holling type III functional response result in the same predation pressure of damselflies on mosquitoes at 749 m elevation for the current climate scenario (see below). At this elevation, mosquitoes are the most abundant prey species (D. Foote, personal communication) and damselflies will have switched to mosquitoes as their only prey. The searching rate of mosquitoes for a Holling type III functional response (sM_L) should then be close to the searching rate for a Holling type II response.

Global warming scenarios

We constructed scenarios for daily temperatures during an average El Niño/La Niña-Southern Oscillation (ENSO) cycle at 13 points along an elevational gradient from 749 to 1,952 m in the Pahala watershed. Each point along the elevational gradient was located in the middle of a 1 km^2 grid cell (Fig. 1). We used ANUSPLIN version 4.2 (Hutchinson) to fit thin plate smooth spline surfaces to weekly temperature data (1980–2004) for weather stations on Hawaii (National Climatic Data Center, USA) and estimated weekly temperatures for the points located in the middle of each grid cell. Daily temperatures were calculated using a Piecewise Cubic Hermite Interpolating Polynomial procedure in Matlab version R2008A (The MathWorks 2008). We used data from the United States Climate Prediction Center to classify each day during the period from 1980 to 2004 as belonging to an El Niño, La Niña, or intermediate period. We used the estimated daily temperatures for each ENSO period to create an "average ENSO cycle" consisting of an average El Niño year, followed by an intermediate year, a La Niña year, and ending with an intermediate year. Each year of the cycle started in July and ended in June. ENSO cycles were repeated to create a 15-year baseline climate scenario for each cell along the elevational gradient in the forest. We also created two climate warming scenarios by adding 1°C and 2°C, respectively, to all daily temperatures in the ENSO cycle. Water temperatures in the rock pools of the forest zone of the Pahala watershed were based on air temperatures (D. Foote, unpublished data), because of the small size of streams and shade provided by the surrounding vegetation.

Model simulations

We simulated the population dynamics of damselflies and mosquitoes at 13 points along an elevational gradient from 749 to 1,952 m in the Pahala watershed. The population dynamics of mosquitoes were simulated both including and excluding predation by damselfly larvae. We used initial values of one adult damselfly and mosquito per liter. Populations were considered extinct when the mean annual density of

reproductive adults declined below 1e-5 individuals per liter. Model simulations were performed in Matlab version R2008A using solver ode45 for ODEs (The MathWorks 2008).

Elasticity analysis

To evaluate how sensitive the percentage reduction in mean adult mosquito densities due to damselfly predation was to changes in the values of parameters, we performed an elasticity analysis (Caswell 2001). The elasticity of a parameter is an indicator of the sensitivity of a certain model prediction to relative changes in this parameter value and was calculated as

$$\text{elasticity} = \frac{dY}{Y_0} \Big/ \frac{dP}{P_0}. \tag{11}$$

In this equation, Y_0 is the percent reduction in mean adult mosquito densities due to damselfly predation using the default values of parameters, P_0 is the default value of the specific parameter for which the elasticity is calculated and dY is the change in Y when the parameter value is changed by dP from 0.75 to 1.25 times P_0. For each parameter setting we performed a 15-year long simulation using the baseline climate scenario for 749 m elevation. Reduction in mean adult mosquito densities due to damselfly predation was calculated over the last ENSO cycle (4 years) of this simulation period.

Results

Temperature variation along the elevational gradient

The average yearly temperature declined from approximately 20°C at 749 m to 14°C at 1952 m in the forest (Fig. 3).

Depending on the elevation, average yearly temperatures during an El Niño event were 0.03–0.16°C higher than during an intermediate period and 0.33–0.57 C higher than during a La Niña event. The warmest months were typically July–September, while the coldest months were January–February (Fig. 3). The difference in mean temperature between the warmest and coldest month in a year was 3.1–3.7°C, depending on the elevation. The mean monthly temperature was usually lowest during a La Niña event, especially for March–August, while the mean temperature during January–March was highest during an El Niño event (Fig. 3).

The effect of temperature on the native predator

Damselfly populations persist across the elevational gradient in the forest for all climate scenarios. Temperature had a consistent positive effect on the abundance of damselfly larvae with higher temperatures increasing their abundance. The density of damselfly larvae decreased with increasing elevation (Fig. 4a). The density of damselfly larvae also varied seasonally, with highest densities during summer to early autumn and lowest densities in winter to early spring; this seasonal pattern was more pronounced at higher elevations (Fig. 4a), but similar for all climate warming scenarios (Fig. 4b). Global warming increased the density of damselfly larvae (Fig. 4b) for all elevations.

The effect of temperature and biotic resistance on the invasive prey

Our model showed that biotic resistance did not change the distribution of mosquitoes along the elevational gradient. Populations with and without damselfly predation persisted to at least 1,952 m for all climate scenarios (Fig. 5a). In the

Fig. 3 Seasonal variation in the temperature at three locations along the elevational gradient in the Pahala watershed on the Island of Hawaii during an El Niño, La Niña, and intermediate period

Fig. 4 Predicted seasonal variation in the density of later instar *M. calliphya* larvae at three locations along an elevational gradient (**a**) and at 749 m elevation for three different climate scenarios (**b**) in the Pahala watershed on the Island of Hawaii. The current climate and the global warming scenarios are indicated by T_0, T_1 (+1°C), and T_2 (+2°C), respectively. Note the scale difference between **a** and **b**
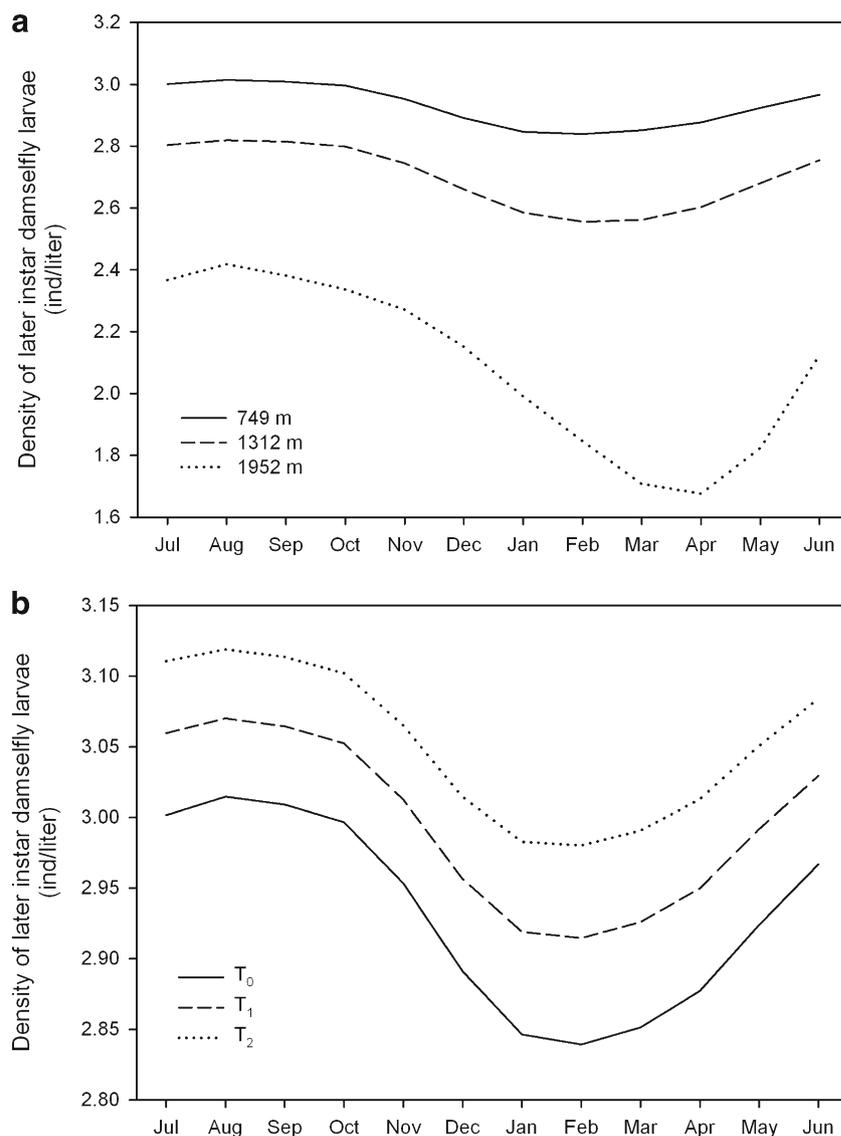

absence of biotic resistance, higher temperatures consistently increased the densities of adult mosquitoes. Biotic resistance by damselflies decreased the abundance of adult mosquitoes, but did not change the qualitative effect of temperature on the abundance of adult mosquitoes. The densities of adult mosquitoes were higher at lower elevations (warmer temperature; Fig. 5a) and varied seasonally with higher densities in summer and lower densities in the winter (Fig. 6a). The density of adult mosquitoes differed little among periods of the ENSO cycle. Global warming increased the densities of adult mosquitoes (Figs. 5a, 6a).

The effect of temperature on biotic resistance

We measured the strength of biotic resistance of the damselfly to the invasive mosquito as the percentage of mosquito population reduction. Temperature had a consistent negative effect on the strength of biotic resistance of the

damselfly to the invasive mosquito with higher temperatures reducing the percent population reduction of the mosquito. The strength of biotic resistance of the damselfly to the invasive mosquito varied with elevation (Fig. 5b), season (Fig. 6b), climate scenario (Figs. 5b, 6b), period within the ENSO cycle, and interactions between these factors. Below, we report ranges for the separate effect of each of these factors on the percent reduction of the mean monthly (for season) or mean annual density of adult mosquitoes (all other factors), for all possible settings of the other factors. Increasing the elevation from 749 to 1,952 m increased the percent reduction of adult mosquito densities in the range of 15–17%. The seasonal difference in the percent reduction of adult mosquito densities was in the range of 1–10%. Global warming of 2°C decreased the reduction of the density of adult mosquitoes due to damselfly predation in the range of 4.3–6.4%. The effect of the ENSO cycle on the reduction of adult mosquito densities by damselflies was in the range of

Fig. 5 Predicted average yearly density of *C. quinquefasciatus* larvae in the presence (**a**) and absence (**b**) of predatory later instar *M. calliphya* larvae and the% reduction in adult *C. quinquefasciatus* populations from predation by *M. calliphya*, along an elevational gradient in the Pahala watershed on the Island of Hawaii for three climate scenarios. The current climate and the global warming scenarios are indicated by T_0, T_1 (+1°C), and T_2 (+2°C), respectively
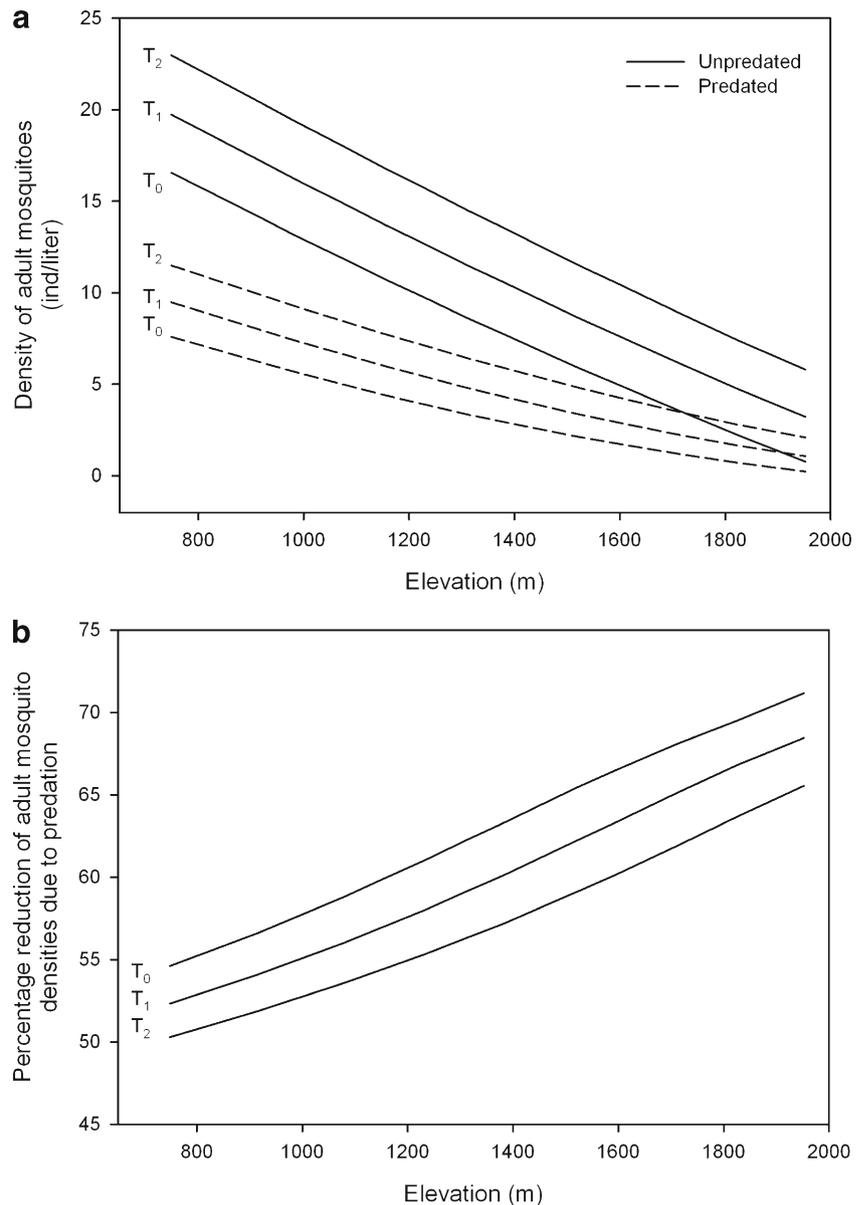
0.58–1.6%; relatively small in comparison with altitude, global warming, and the seasonal cycles.

Elasticity analysis

Analyses indicated that the strength of biotic resistance of the damselfly to the invasive mosquito (measured by percent population reduction of the mosquito) was most sensitive to changes in the carrying capacity of damselfly larvae and development rate of mosquito larvae (Table 2). Increasing the carrying capacity of damselfly larvae or decreasing the development rate (increasing development time) of mosquito larvae increased the strength of biotic resistance of the damselfly to the mosquito. The impact of predation was moderately sensitive to changes in search rate, carrying capacity of mosquito larvae, development rate of damselfly

larvae, and the fraction of the larval stage of damselflies that is spent as early instars. Higher search rates and earlier transition of damselfly larvae to the predatory stage increased the rate of mosquito predation. Increasing the carrying capacity for mosquito larvae lowered the impact of predation. Predation was least sensitive to changes in parameters that directly affect the dynamics of the egg, pre-reproductive, and reproductive stages of damselflies.

Discussion

We developed a mathematical model to study the effect of global warming on biotic resistance of a native predator to an introduced prey in an aquatic insect ecosystem. As a relatively simple model system, we used the rock pool

Fig. 6 Seasonal variation in the density of adult *C. quinquefasciatus* in the absence and presence of predatory later instar *M. calliphya* (**a**) and the% reduction in adult *C. quinquefasciatus* populations as a result of predation by *M. calliphya* (**b**) at 749 m elevation in the Pahala watershed on the Island of Hawaii for three climate scenarios. The current climate and the climate change scenarios are indicated by T_0, T_1 (+1°C), and T_2 (+2°C), respectively
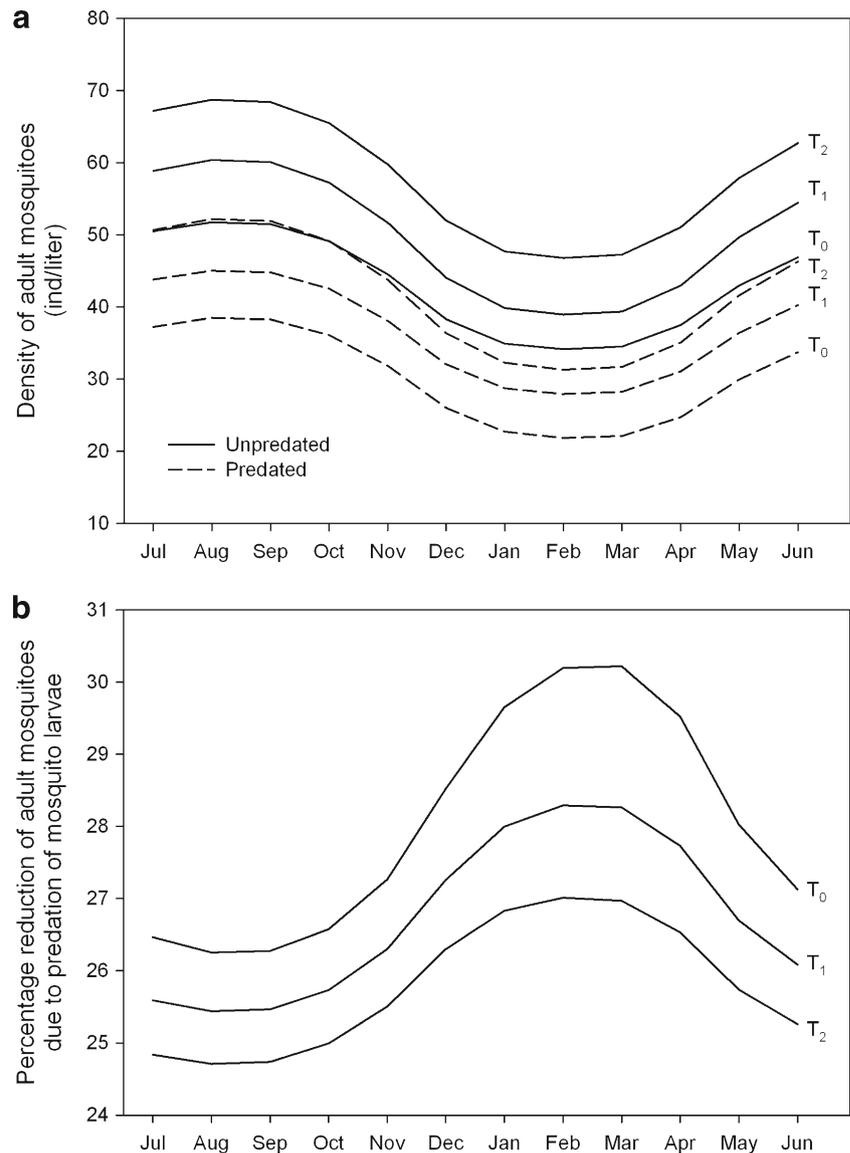
community in streams in montane rainforests on the Island of Hawaii. In these rock pools, the damselfly *M. calliphya* is the top predator and the most abundant prey species is the invasive mosquito *C. quinquefasciatus*, which is the primary vector of avian malaria. Our results suggest that global warming may decrease the impact of biotic resistance by native predators and lead to future increases in the abundance of invasive mosquitoes.

Explanation of the model predictions

Higher temperatures increase the metabolic rate of aquatic insects, which shortens their maturation time and can increase their reproduction rate (Gillooly et al. 2002; Brown et al. 2004). In addition, when the mortality rate is constant, a shorter maturation time leads to a higher percentage of individuals that survive to the reproductive stage. The

reproductive output of a population per unit time therefore increases with increasing temperature, which results in a higher abundance (Savage et al. 2004). This explains why the abundance of the predator increases with increasing temperature in our model system. A higher metabolic rate also increases the per capita consumption rate of prey. The combination of a higher predator abundance and higher per capita consumption results in increased predation of the prey species. However, in aquatic insect ecosystems, as is the case for the predator, a higher temperature also shortens the maturation time of a prey species and increases its reproduction rate. Whether the increase in the reproductive output of individual prey with increasing temperature outweighs the increase in the consumption rate of prey depends on the relative sensitivity of the predator and prey demographic rates, the effect of temperature on predator search rate and handling time of prey and the carrying capacity of the

Table 2 The elasticity of the mean % reduction of adult mosquito densities due to damselfly predation during an average year at 749 m elevation to changes in the model parameters

Parameter	Elasticity	Sign
K_{D_L}	4.05e-1	+
$1/d_{M_L}(T)$	3.90e-1	+
s	3.30e-1	+
K_{M_L}	2.54e-1	+
$1/d_{D_L}$[a]	1.94e-1	−
α	1.47e-1	−
$\mu_{D_{LL}}$	1.17e-1	−
$h(T)$	7.77e-2	−
$1/\mu_{M_R}$	3.96e-2	−
l_M	3.63e-2	+
$\mu_{D_{LE}}$	3.01e-2	−
c_M	3.01e-2	−
l_D	2.48e-2	+
$1/\mu_{D_R}$	2.27e-2	−
c_D	2.11e-2	+
μ_{M_L}	1.47e-2	−
μ_{M_E}	9.29e-3	+
$1/d_{D_E}$	9.26e-3	+
μ_{D_E}	6.73e-3	−
$1/d_{D_E}$	6.67e-3	−
μ_{D_P}	3.34e-3	−
$1/d_{D_P}$	3.32e-3	−

The sign in column 3 indicates whether this percentage reduction increases (+) or decreases (−) when the parameter value increases. The elasticity analysis was conducted using the current climate scenario. Using the default values in Table 1 resulted in a reduction of adult mosquito densities due to damselfly predation of 53.5%

[a] We varied the development rate of early and later instar damselfly larvae simultaneously, because they were assumed to depend on each other

predator and prey species. In our model system, the increase in the reproductive output of individual prey with increasing temperature outweighs the increase in the consumption rate of prey. This explains why higher temperatures increase the abundance of the prey species and reduce the impact of the predator on the prey population (measured as the % population reduction). Our elasticity analysis shows that the carrying capacity of the damselfly larvae and the length of the immature mosquito stage have an important effect on the balance between the reproductive output and predation rate of prey in our model system.

Comparison with literature

Our results suggest that biotic resistance of a native predator to invasive prey may significantly reduce the abundance of the invasive prey species in cold-blooded systems. This is in agreement with other studies for a variety of ecological settings (Gruner 2005; deRivera et al. 2005; Carlsson et al. 2009; Dumont et al. 2011). However, studies that determine the impact of temperature on biotic resistance of a native predator to an invasive prey are rare. Veiga et al. (2011) reported that the consumption rate of an invasive mussel by a native crab tended to decrease with increasing temperature, when it was the only available prey species, while the consumption rate of a native mussel tended to increase with increasing temperature. This differs from our observations that the consumption rate of mosquito larvae by damselfly larvae increased with increasing temperature (D. Foote, unpublished data). To the best of our knowledge, there are no studies that determine the effect of temperature on the reduction in the abundance of an invasive prey by a native predator in aquatic insect ecosystems. Our model suggests that future warming could increase the abundance of invasive mosquitoes and may allow them to expand to higher elevations. This is in agreement with predicted increases in altitudinal range for many aquatic insects and other invertebrates in response to recent climate warming (Walther et al. 2002; Eyre et al. 2005; Hickling et al. 2006; Musolin 2007).

Generality of the model predictions

The impact of changes in the predation pressure on an invasive species due to global warming will depend on whether predation is a limiting factor on prey abundance. If predation is limiting, our study shows that global warming may allow the prey to escape from predator control. However, there are a number of factors that could influence the effect of global warming on the level of biotic resistance. First, the effect of global warming will depend on the life history of predator(s) and invasive prey and how these are affected by temperature. Second, the carrying capacity of the predator and prey species may also play an important role. If predators have reached carrying capacity and it is not increased due to global warming, this will limit the impact of predators on invasive prey (our model system). However, if the invasive species reaches it carrying capacity earlier than the predator, global warming may increase biotic resistance. Third, in our model, the predator is a generalist and we use a Holling type III functional response (Holling 1959) so that predators may consume other prey, when the abundance of the invasive species is low. This absence of a numerical response by the predator could overestimate total prey consumption. Fourth, next to temperature, photoperiod may also be an important factor regulating the development of aquatic insects in temperate systems (Corbet 1999; Musolin 2007). Finally, in ecosystems, which are more complex than our model system, global warming may change the abundance of the predator through interactions with other species in the community (Montoya and Raffaelli 2010).

More research is needed to determine how these factors interact with global warming to affect biotic resistance of native predators to invasive prey.

Consequences of decreased biotic resistance for disease transmission

When an invasive species also transmits disease, reduced biotic resistance may have important consequences for disease transmission in ecological, domestic animal, and human systems (Harvell et al. 2002). The invasive prey species in our model system, *C. quinquefasciatus*, is a vector of avian malaria, which is considered a primary factor contributing to population declines and changes in the distribution of native Hawaiian forest birds (van Riper et al. 1986, van Riper 1991; Samuel et al. 2011). The elevational distribution of mosquitoes, and therefore potential transmission of avian malaria to endangered Hawaiian forest birds, is limited by cooler temperatures that reduce vector and parasite development (Ahumada et al. 2004; Benning et al. 2002; LaPointe 2000; LaPointe et al. 2010; Samuel et al. 2011). For successful disease transmission, the development time of *Plasmodium relictum* must be shorter than the longevity of adult mosquitoes (LaPointe et al. 2010). Based on the average longevity of 14 days (Table 1), a lower threshold temperature of approximately 13°C, and a cumulative thermal requirement for avian malaria development of 84° days, most mosquitoes will not be able to transmit avian malaria above approximately 1,300 m (Ahumada et al. 2004; Benning et al. 2002; LaPointe 2000; LaPointe et al. 2010). Nonetheless, transmission at higher altitudes is possible during warmer seasons of the year if adult mosquitoes survive long enough to allow parasite development.

Native damselfly distributions overlap with mosquitoes, but extend to 2,000 m (D. Foote, unpublished data). Our model simulations predict that predation by native damselflies reduces the abundance of adult mosquitoes by 55% at 749 m and 71% at 1952 m elevation. This reduction in mosquito density by damselfly predation may reduce the year-round transmission of avian malaria to susceptible Hawaiian honeycreepers in forest ecosystems below 1,300 m or the seasonal transmission during summer–fall at higher elevations.

Hawaii's tropical montane cloud forests are thought to be especially vulnerable to climate change (Loope and Giambelluca 1998) with increases of 0.27°C per decade at higher elevations during the period 1976–2006 (Giambelluca et al. 2008). Our model simulations indicate global warming should increase the abundance of mosquitoes in areas with sympatric damselflies, potentially increasing the transmission of avian malaria to susceptible Hawaiian birds. In these areas, global warming could also favor a more rapid development of malaria parasites (LaPointe 2000; Benning et al. 2002;

Ahumada et al. 2004; LaPointe et al. 2010), which in combination with higher mosquito density could have a negative impact on high elevation bird populations.

Conclusions

Our modeling study indicates that climate warming may affect biotic resistance to invasive species by differentially affecting the demographic responses of native predator and exotic prey to temperature. Predicted patterns of global warming could release invasive prey species from predation pressures in cold-blooded systems. This may contribute to increases in the abundance and the expansion of the distribution of invasive species. If the invasive species is a disease vector, this will likely increase the distribution and incidence of diseases, which may increase the impact of both human and wildlife diseases.

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