Technical Report HCSU-077

PROGRAM MAMO: MODELS FOR AVIAN MANAGEMENT OPTIMIZATION - USER GUIDE

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CHAPTER 1: A QUICK INTRODUCTION TO MAMO

Hawai‘i is the most remote archipelago on earth, resulting in the highest percentage of land-based endemic birds anywhere in the world. Unfortunately, Hawaiian birds have suffered dramatic losses since the arrival of people 800–1200 years ago: entire taxonomic groups have disappeared, such as flightless rails, waterfowl and a whole passerine family (Hawaiian honeyeaters), while others have lost much of their initial diversity. For instance, only 17 species (one-third) of Hawaiian honeycreepers remain, 10 of which are threatened with imminent risk of extinction, being listed as 'Endangered' or 'Critically Endangered' by the International Union for Conservation of Nature.

We developed and present in this manual an R-based program that can evaluate the relative importance of different threats to forest birds as well as the effectiveness of various management actions to mitigate the threats. Our application of the model has focused on Hakalau Forest National Wildlife Refuge on Hawai‘i Island, but the program is designed to be flexible and can be used in other areas across Hawai‘i and beyond. Importantly, the program was designed as an adaptive management tool for managers, allowing non-modelers to update information, design simulations, and obtain meaningful output to help guide conservation efforts. We named our software MAMO, based on the name of the extinct Hawaiian honeycreeper mamo (Drepanis sp.) and an acronym for 'Models for Avian Management Optimization'.

Our intent is for MAMO to continue to be improved, both by ourselves and other researchers, as a shared resource for the Hawaii forest bird research and management community, and beyond. As such, this version of MAMO is the first iteration, a fully developed model that nonetheless has much room to grow. MAMO’s complexity is an asset to investigate a variety of scientific and applied questions, but it is also a weakness in the sense that we were unable to test its behavior under all the possible scenarios. Despite our best efforts, bugs are possible, and the program comes with no guarantee. In addition, the code is not always optimal in terms of both efficiency and homogeneity, it is not always as simple as it could be for users, and it is not as flexible as it could be (for instance, hard code modification is necessary to introduce new data sets in the present version). Despite these potential shortcomings, we believe that MAMO fills an important gap in the current tool set available to researchers and managers in Hawai‘i. It has already been used to produce exciting new insights into the dynamics and conservation of Hawaiian native birds, and the program is continuing to be applied to new questions of conservation interest.

1.1 Overview
The following chapters describe the structure and code of MAMO, and walk the reader through running the different components of the program with sample data. This manual should be used alongside a computer running R, so that the reader can copy and paste code into R, observe the output, and follow along interactively. Taken together, chapters 2–4 will allow the user to replicate a simulation study investigating the consequences of climate change and two potential management actions on the population dynamics of a vulnerable and iconic Hawaiian forest bird, the ‘I‘iwi (Drepanis coccinea; hereafter IIWI).

Chapter 2 is devoted to describing the core function of the program, mamo, a function that simulates the life-history of individuals belonging to a set of populations arranged on a spatial grid, and potentially connected by seasonal migrations and dispersal. While mamo can be called
on its own, other R functions such as `f.calibr` and `f.run` are generally used to call `mamo` and perform a batch of simulations exploring different parameter combinations.

**Chapter 3** describes the calibration of `mamo` parameters. We describe the tools we developed (including `f.calibr`) to determine a set of parameter values capable of replicating the current pattern of distribution of the study species (in this case, IIWI) along an elevational gradient. This step is critical in order to obtain meaningful output when predicting the impact of future climatic conditions or a given management action. In essence, if we cannot predict the present, how can we expect to predict the future?

**Chapter 4** details how to design and conduct a simulation study. We present the tools available (including `f.run`) to run a series of simulations covering the full spectrum of scenarios that we want to investigate while accounting for parameter uncertainty via what we call the ‘demographic envelop’. A series of graphical tools are also presented in order to help the user interpreting the simulation results.

Additional information on the project, including the mathematical underpinning of MAMO, are described in Guillaumet et al. 2017, referred to in this manual as the 'IIWI paper'. Appendix 1 has an unformatted copy of the published paper.


**1.2. The R language**

We developed MAMO with R version 3.2.0. R is a free open source software for data analysis, statistical computing, and graphics (Sanchez 2013). It is also a programming language ideal for the creation and manipulation of functions. We designed MAMO as the equivalent of an R package, containing reusable R functions together with the documentation necessary to understand how to use them. Our hope is that MAMO becomes a full R package in the future.

Although learning R is not required to use MAMO, it is very helpful and we strongly recommended it. Self-teaching is an option, and below are a few lectures that are available online. Good luck!

https://www.stat.berkeley.edu/~spector/Rcourse.pdf

https://cran.r-project.org/doc/contrib/Paradis-rdebut_en.pdf

**Chapter 2: The Basic MAMO Function: mamo**

The function `mamo` is at the core of the program. As we previously mentioned, it is the function actually simulating the life-history of individual e-birds (simulated birds in the model). Please refer to the 'IIWI paper' for a description of the mathematics underlying the function.
2.1 The arguments of *mamo*

Arguments, or variables of the model simulation, are assigned by the user, and describe the spatial and temporal extent of the simulation, and key demographic attributes of the species. For descriptive and practical purpose, the arguments are grouped into several classes, such as spatial structure and time frame. In the sections below, we present each argument (variable used by the function whose value can be modified by the user) using the following components: definition of the argument, range of values it can take as well as an example (Ex), and a notes section to highlight potential misuse, unexpected interaction with other parameter values, and other important information.

### 2.1.1 Spatial structure variables

<table>
<thead>
<tr>
<th>Argument</th>
<th>Definition</th>
<th>Value</th>
<th>Ex</th>
<th>Note</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>nr</strong></td>
<td>Number of rows of the spatial grid. Each row represents a single elevational band.</td>
<td>$\mathbb{N}^+$ = {1, 2, ...}.</td>
<td>$nr = 10$</td>
<td>Simulation time is positively related to the dimension of the grid, and large grids could require long computing time.</td>
</tr>
<tr>
<td><strong>nc</strong></td>
<td>Number of columns of the spatial grid.</td>
<td>$\mathbb{N}^+$ = {1, 2, ...}.</td>
<td>$nc = 2$</td>
<td>1) Simulation time is positively related to the dimension of the grid, and large grids could require long computing time. 2) We recommend using 2 or 3 columns at least. Immigration from adjacent cells is an important feature of the model, such that cells without neighboring cells will tend to receive fewer migrants. This effect is attenuated as the number of columns increase.</td>
</tr>
<tr>
<td><strong>grad</strong></td>
<td>The elevational range of the spatial grid (in meters), starting with the highest elevation. This argument is used for producing figures and calculating summary statistics.</td>
<td>Max and min elevations for consideration</td>
<td>$grad = c(1900, 1000)$</td>
<td></td>
</tr>
<tr>
<td><strong>unit</strong></td>
<td>Dimension of each grid cell (patch), each a square with side = unit km.</td>
<td>User defined</td>
<td>$unit = 1$</td>
<td>1) For our analyses on windward Mauna Kea, $unit = 1$ (patch = 1 Km$^2$) covered an elevational band of approximately 100 m. 2) The value of $unit$ seems to affect the capacity of the &quot;fast.risky&quot; option of <em>calc.gamma.d</em> to generate meaningful outputs. Always check the output parameter <em>test.disp.breed</em> when using &quot;fast.risky&quot; (see chapter 2.3).</td>
</tr>
</tbody>
</table>

MAMO does not require the user to enter spatially explicit data for the arguments of other classes. Four options are possible, and MAMO will automatically spread the values entered into
each of the spatial grid cell. Unless stated otherwise, our examples for the remaining arguments correspond to a spatial grid (called \(sg\)) of 4 patches distributed over 2 rows and 2 columns (note some variables introduced here are fully explained later in report). In this case, A and C are at higher elevation than B and D; as in R columns are filled in first, A corresponds to patch 1 (i.e. \(sg[1]\)), B to patch 2, C to patch 3 and D to patch 4.

\[
[A] [C] \\
[B] [D]
\]

1) When a single value is entered, the single value is spread into each grid cell.
Ex: for the parameter \(t.b\), the value \(t.b = 242\) will yield the matrix:

\[
[242] [242] \\
[242] [242]
\]

2) When a vector of length \(nr\) is entered, the vector is distributed over the \(nc\) columns.
Ex: for the parameter \(t.b\), the value \(t.b = c(242, 300)\) will yield the matrix:

\[
[242] [242] \\
[300] [300]
\]

3) A vector of length \(nr \times nc\) can be entered.
Ex: for the parameter \(t.b\), the value \(t.b = c(242, 300, 150, 355)\) will yield the matrix:

\[
[242] [150] \\
[300] [355]
\]

4) A matrix can be entered.
Ex: for the parameter \(t.b\), the value \(t.b = \text{matrix}(c(242, 300, 150, 355), nr = 2, nc = 2)\) will yield the matrix:

\[
[242] [150] \\
[300] [355]
\]

### 2.1.2 Time frame variables

\(T\)

**Definition:** Number of years of simulation.

**Value:** \(\in \mathbb{N}^+ = \{1, 2, \ldots\}\).

**Ex:** \(T = 60\)

**Note:** Simulations need enough years for population dynamics to stabilize under set parameters. Graphical and numerical tools are available to help choose a particular value (see chapter 2.2.1).

\(Tm\)

**Definition:** \(Tm\) is the number of years before individuals are exposed to Malaria and rat predation. These are introduced in the simulations at year \(Tm + 1\). Simulation time prior to \(Tm\) is important for reaching an equilibrium, in particular concerning the proportion of each age class.

**Value:** \(\in \mathbb{N}^+ = \{1, 2, \ldots\}\).

**Ex:** \(Tm = 5\)

**Note:**

1) \(Tm\) must be \(\leq T\). If \(Tm = T\), all simulations are run without malaria (and rat predation).
2) We recommend choosing \( Tm \) such as:

i) \( Tm \geq 2 \) (at least, to allow for populations to reach equilibrium post starting conditions).

ii) \( T - Tm > 50 \).

---

**Definition:** Duration of the breeding season (in number of days).

**Value:** \([1, 365] \ (\in \mathbb{N}^+\)\)

**Ex:** \( t.b = 242 \)

**Note:**

1) \( t.b = 365 \) is used for non-migratory species.

2) Two distinct non-breeding seasons have been recognized for IIWI ('IIWI paper'), and presumably for APAP which shares a similar ecology. When the user chooses a value of \( t.b < 365 \), the current version of \( mamo \) switches to a 3-season model, with one breeding and two non-breeding seasons. Hence, at least one day per non-breeding season should be allowed, and therefore \( t.b \leq 363 \) for migratory species.

2) Although \( mamo \) was designed to accommodate variation in phenology across the gradient, no specific testing of the model behavior was performed in such conditions.

---

**Definition:** Proportion of the non-breeding season (lasting 365 - \( t.b \)) spent in the first non-breeding patch.

1) **Value:** \((0 < x < 1)\) for migratory species, NA for non-migratory species

**Ex:** \( f.nb.1 = 0.5 \)

**Note:**

1) While any value could be chosen for non-migratory species, we recommend using \( f.nb.1 = NA \) because the parameter is irrelevant.

2) In the current \( mamo \) version, only one- or three-season designs are allowed, so \( f.nb.1 \) cannot equal zero or one (both corresponding to two seasons).

---

**Definition:** Lower bound of fledging time (number of days after beginning of breeding season).

**Value:** \([1, t.b] \ (\in \mathbb{N}^+)\) if \( reproduction.malaria = "simple"\)

**Ex:** \( min.fledg = 100 \)

**Note:** If \( reproduction.malaria = "complex"\), then value = \([1, t.b-14] \ (\in \mathbb{N}^+)\); make sure \( min.fledg < peak.fledg \times t.b < t.b - 14 \) (about two weeks after fledging, dependent juveniles become very mobile and can leave the breeding territory with adult).

---

**Definition:** Peak of fledging time (derived as a proportion of the total days in breeding season).

**Value:** \((0<x<1)\)

**Ex:** \( peak.fledg = 0.67 \)

**Note:** If either \( reproduction.malaria = "simple"\) or \( SD.fledg = 0 \), the fledging date is calculated as \( peak.fledg \times t.b \); otherwise, the fledging date is derived from a truncated normal distribution with mean \( peak.fledg \times t.b \).

---

**Definition:** Standard deviation of fledging time.
Definition: Standard deviation around peak.fledg (in days).
Value: $\in \mathbb{R}_0^+$ (0 and positive values)
Ex: $SD.fledg = 20$

Note: When reproduction.malaria = "complex" and $SD.fledg \neq 0$, the fledging time is calculated based on a truncated normal distribution with min = min.fledg, mean = peak.fledg $\times$ t.b, max = t.b - 14, and standard deviation = $SD.fledg$. Preliminary assessments suggested that the actual mean of the distribution differed notably from the expected mean (peak.fledg $\times$ t.b) when $SD.fledg$ was large; further debugging is necessary.

2.1.3 Initial conditions variables

<table>
<thead>
<tr>
<th>init.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Definition: Initial number of one-year old individuals per patch.</td>
</tr>
<tr>
<td>Value: $\in \mathbb{N}^+$</td>
</tr>
<tr>
<td>Ex: $init.1 = 50$</td>
</tr>
<tr>
<td>Note:</td>
</tr>
<tr>
<td>1) We recommend starting simulations at or near carrying capacity, for example by choosing $init.1 = init.2 = \text{half of the carrying capacity}$ each. Note, due to program language limitations, $init.1 = K.b / 2$ cannot be used to initialize MAMO. If $K.b = 200$, then use $init.1 = 100$ and $init.2 = 100$.</td>
</tr>
<tr>
<td>2) If initial values are chosen too far from carrying capacity, it may take more time to build up numbers than model simulation runs, and the dynamics measured at $T$ might still be transient.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>init.2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Definition: Initial number of individuals $\geq$ 2-year old per patch.</td>
</tr>
<tr>
<td>Value: $\in \mathbb{N}^+$</td>
</tr>
<tr>
<td>Ex: $init.2 = 50$</td>
</tr>
<tr>
<td>Note:</td>
</tr>
<tr>
<td>1) We recommend starting simulations at or near carrying capacity, for example by choosing $init.1 = init.2 = \text{half of the carrying capacity}$ each. Note, due to program language limitations, $init.1 = K.b / 2$ cannot be used to initialize MAMO. If $K.b = 200$, then use $init.1 = 100$ and $init.2 = 100$.</td>
</tr>
<tr>
<td>2) If initial values are chosen too far from carrying capacity, it may take more time to build up numbers than model simulation runs, and the dynamics measured at $T$ might still be transient.</td>
</tr>
</tbody>
</table>

2.1.4 Survival variables

<table>
<thead>
<tr>
<th>s.ad</th>
</tr>
</thead>
<tbody>
<tr>
<td>Definition: Baseline annual survival rate of adults (not including the effect of malaria or rat predation).</td>
</tr>
<tr>
<td>Value: $[0,1]$</td>
</tr>
<tr>
<td>Ex: $s.ad = 0.8$</td>
</tr>
<tr>
<td>Note: The parameter corresponds to true survival, and not apparent survival (See e.g. Gilroy et al. 2012 for definitions).</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>rat.s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Definition: Proportion of breeding females killed by rats; rat.s is such that the actual survival probability of females is multiplied by the coefficient (1-rat.s).</td>
</tr>
<tr>
<td>Value: $[0,1]$</td>
</tr>
</tbody>
</table>
Ex: $rat.s = 0.05$
Note: We assume that $rat.s \leq rat.f$ (reductions in fecundity by rats) for calibration purpose. Parameter combinations not respecting this inequality are automatically discarded during the calibration run. However, no such automatic constraint is present when running a single run of MAMO, so the user can actually choose $rat.s > rat.f$ if there is biological evidence of such a relationship.

### s.juv

**Definition:** Baseline survival rate of juveniles from fledging to next year’s breeding season (not including the effect of malaria or rat predation).

**Value:** $[0,1]$

**Ex:** $s.juv = 0.4$

**Note:**
1) In the absence of better information, we recommend using a value equivalent to one half $s.ad$ (e.g., Gardali et al. 2003).
2) Note that $s.juv = s.ad / 2$ cannot be used to initialize MAMO (due to program constraints). If $s.ad = 0.729$, then use $s.juv = 0.729 / 2$, or 0.3645.

### 2.1.5 Reproduction and habitat quality variables

### fec

**Definition:** Baseline (malaria- and density-independent) number of female offspring fledged per female $\geq 2$-year old during a single breeding season.

**Value:** $\in \mathbb{R}^+$

**Ex:** $fec = 1.54$

**Note:** During the calibration process, we assume that $fec.1 \leq fec$. Parameter combinations not respecting this inequality are automatically discarded during the calibration run. However, no such automatic constraint is present when running a single run of MAMO, so the user can actually choose $fec.1 > fec$ (but biologically unlikely; e.g., Woodworth & Pratt 2009).

### fec.1

**Definition:** Baseline (malaria- and density-independent) number of female offspring fledged per female 1-year old during a single breeding season.

**Value:** $\in \mathbb{R}^+$

**Ex:** $fec.1 = 0.49$

**Note:** During the calibration process, we assume that $fec.1 \leq fec$. Parameter combinations not respecting this inequality are automatically discarded during the calibration run. However, no such automatic constraint is present when running a single run of MAMO, so the user can actually choose $fec.1 > fec$ (but biologically unlikely; e.g., Woodworth & Pratt 2009).

### rat.f

**Definition:** Proportion of juveniles killed by rats.

**Value:** $[0,1]$

**Ex:** $rat.f = 0.07$

**Note:** We assume that $rat.s \leq rat.f$ for calibration purpose. Parameter combinations not respecting this inequality are automatically discarded during the calibration run. However, no such automatic constraint is present when running a single run of MAMO, so the user can actually choose $rat.s > rat.f$ if there is biological evidence of such a relationship.
**K.b**

**Definition:** Carrying capacity (maximum number of breeding pairs) of a single patch.

**Value:** $\in \mathbb{N}^+$

**Ex:** $K.b = 600$

**Note:**
1) $K.b$ should be set with consideration of patch size (unit).
2) The behavior of the model has not been tested at very low densities ($K.b < 4$), and some erratic or unexpected behavior may arise; further developments will be necessary to account for irregular landscapes including patches with $K.b = 0$.

**thr.DD**

**Definition:** Threshold (number of pairs per patch) above which automatic density-dependent reduction in fecundity occurs (see 'IIWI paper' for details).

**Value:** $\in \mathbb{N}^+$

**Ex:** $thr.DD = 300$

**Note:**
1) We recommend using a value equivalent to $K.b / 2$ (e.g., Frederiksen et al. 2001).
2) Note that $thr.DD = K.b / 2$ cannot be used to initialize MAMO due to programing limitations. If $K.b = 580$, then use $thr.DD = 290$.
3) $thr.DD \leq K.b$

**K.nb.1**

**Definition:** Patch quality (food abundance) during the 1$^{st}$ period of the non-breeding season.

**Value:** See below

**Ex:** $K.nb.1$ (from 2003, see IIWI paper) = c(2.45556, 3.23333, 4.01111, 4.78889, 5.56667, 6.05000, 9.81667, 17.52500, 19.12000, 17.33333) corresponding to grad = c(1900, 1000).

**Note:** Although the function `mamo` can accommodate any $K.nb.1$ value, other functions involved in calibration and simulation studies currently can only recognize the $K.nb.1$ values included in the data file associated with the program (called 'm3_data.r'); greater flexibility may be allowed in future MAMO versions.

**K.nb.2**

**Definition:** Patch quality (food abundance) during the 2$^{nd}$ period of the non-breeding season.

**Value:** See below

**Ex:** $K.nb.2$ (see IIWI paper) = c(4.06815, 7.07556, 10.08296, 13.09037, 16.09778, 19.16667, 7.47778, 4.55000, 4.16667, 2.36667) corresponding to grad = c(1900, 1000).

**reproduction.malaria**

**Definition:** This parameter offers two similar yet distinct algorithms to account for the fact that newly infected e-birds should have, everything else being equal, a lower reproductive success than other categories.

**Value:** "simple" or "complex"

**Ex:** `reproduction.malaria = "simple"`

**Note:**
1) We recommend using the "simple" version because it is much faster and has provided us with very similar results in the simulations conducted thus far.
2) The complete life-history information of all individuals, including their lifetime patch occupancy and reproductive output, can be stored and obtained at the end of the simulation using the "complex" algorithm.

2.1.6 Malaria variables

**alpha.b**

*Definition:* Daily probability of infection of a susceptible e-bird during the breeding season.

*Value:* See below

*Ex:* 

\[
\text{alpha.b} = c(0.00000e+00, 0.00000e+00, 3.21323e-06, 6.42646e-06, 1.40851e-03, 3.37271e-03, 5.89904e-03, 8.98748e-03, 1.29177e-02, 1.34780e-02)\]

Note: Currently available data sets, alpha.b (above) and alpha.b.2100, have been estimated for the period going from September 1st to April 30th (corresponding to \(t.b = 242\), used for IIWI and APAP).

**alpha.nb.1**

*Definition:* Daily probability of infection of a susceptible e-bird during the 1st period of the non-breeding season.

*Value:* See below

*Ex:* 

\[
\text{alpha.nb.1} = c(0.00000e+00, 0.00000e+00, 1.61291e-08, 3.22581e-08, 7.02270e-04, 1.68541e-03, 2.94945e-03, 4.49439e-03, 6.46068e-03, 6.74157e-03)\]

Note: Currently available data sets used for IIWI and APAP, alpha.nb.1 (above) and alpha.nb.1.2100, have been estimated for the May–June period corresponding to \(f.nb.1 = 0.5\) (technically, they were actually estimated for the May 1st to July 1st period due to rounding code used, which could be changed in future versions).

**alpha.nb.2**

*Definition:* Daily probability of infection of a susceptible e-bird during the 2nd period of the non-breeding season.

*Value:* See below

*Ex:* 

\[
\text{alpha.nb.2} = c(0.00000e+00, 0.00000e+00, 6.92295e-05, 1.38459e-04, 2.92186e-03, 6.84632e-03, 1.19118e-02, 1.81184e-02, 2.60054e-02, 2.71084e-02)\]

Note: Currently available data sets used for IIWI and APAP, alpha.nb.2 (above) and alpha.nb.2.2100, have been estimated for the July–August period corresponding to \(f.nb.1 = 0.5\) (technically, they were actually estimated for the July 2nd to August 31st period due to rounding code used, which could be changed in future versions).

**Sm.ac**

*Definition:* Probability of surviving acute malaria infection.

*Value:* \([0,1]\)

*Ex:* 

\[
\text{Sm.ac} = 0.13
\]

Note:
1) If they survive the first, acute infection, e-birds are assumed to be immune to subsequent infections.
2) Current version of *mamo* does not allow for spatial variation in this parameter.

### 2.1.7 Movement variables

<table>
<thead>
<tr>
<th><strong>gamma.mov</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Definition:</strong> Parameter controlling the extent of seasonal ('migratory') movements between patches.</td>
</tr>
<tr>
<td><strong>Value:</strong> [-10,10]</td>
</tr>
<tr>
<td><strong>Ex:</strong> <em>gamma.mov</em> = 0.541, the probability to reach a given (equivalent) patch is multiplied by 3/4 every time distance increases by one km.</td>
</tr>
<tr>
<td><strong>Note:</strong></td>
</tr>
<tr>
<td>1) Can take a continuum of values between -10 (no 'net' movement, i.e. roosting always in the breeding patch) and +10 which corresponds to an ideal-free distribution (no resistance to movement / distance does not impede movement). For intermediate values, birds tend to spend the night closer to their breeding patch than expected based on resources alone due to the combined effects of partial resistance to movements and / or partial commuting.</td>
</tr>
<tr>
<td>2) The larger the <em>gamma.mov</em> value, the greater the propensity to 'migrate' and stay (including at night) near higher quality patches. We therefore regard <em>gamma.mov</em> as an index of migration propensity.</td>
</tr>
<tr>
<td>3) The current version of <em>mamo</em> does not allow for spatial variation in this parameter.</td>
</tr>
<tr>
<td>4) The current version only applies to IIWI and APAP (as determined by <em>t.b</em> &lt; 365; see argument <em>t.b</em> for further explanations). For other species, any value can be entered, but we recommend using <em>gamma.mov</em> = NA.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>calc.gamma.d</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Definition:</strong> Algorithm used to calculate the hidden parameter <em>gamma.d</em>, which comes from a negative exponential distribution used to shuffle the dispersing fraction <em>fraction.disp</em> into neighboring patches; <em>fraction.disp</em> depends in particular on the parameters <em>fidelity.ad</em> for adults and <em>m.natal</em> for juveniles, but patch dimensions are also important (see also 'IIWI paper' and chapter 2.3 for more details).</td>
</tr>
<tr>
<td><strong>Value:</strong> Currently, can take one of two values: &quot;fast.risky&quot; or &quot;slow.robust&quot;</td>
</tr>
<tr>
<td><strong>Ex:</strong> <em>calc.gamma.d</em> = &quot;fast.risky&quot;</td>
</tr>
<tr>
<td><strong>Note:</strong> As the name implies, &quot;slow.robust&quot; is slow but should always give a meaningful result. Limited testing suggests that the much faster &quot;fast.risky&quot; works well when unit = 1, but not necessarily with other values (further developments required). Always check the output parameter <em>test.disp.breed</em> when using &quot;fast.risky&quot; (see chapter 2.3).</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>n.sim.disp</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Definition:</strong> The number of dispersal events simulated to estimate <em>fraction.disp</em>, the proportion of e-birds leaving a given patch. Each dispersal event is a random draw based on <em>fidelity.ad</em> (for adults), or <em>m.natal</em>, <em>SD.natal</em> and <em>psi.DD</em> (for juveniles).</td>
</tr>
<tr>
<td><strong>Value:</strong> ∈ N*</td>
</tr>
<tr>
<td><strong>Ex:</strong> <em>n.sim.disp</em> = 10,000</td>
</tr>
<tr>
<td><strong>Note:</strong> We recommend using values ≥ 1000, in order to have a decent sample size.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>R.ter</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>R.ter</strong></td>
</tr>
</tbody>
</table>

10
**Definition:** Dimension of the breeding territory (disk radius, in km).

**Value:** $\in \mathbb{R}^+$

**Ex:** $R_{ter} = 0.0234$

**Note:**
1) Current version of *mamo* does not allow spatial variation in this parameter.
2) $R_{ter}$ is generally estimated at relatively high density (see the 'IIWI' paper for details).
   Density-dependence could be accounted for in future versions.

---

**fidelity.ad**

**Definition:** Probability of an adult breeding in year $t+1$ within the same breeding territory as in year $t$.

**Value:** $[0,1]$

**Ex:** $fidelity.ad = 0.95$

**Note:**
1) Current version of *mamo* does not allow spatial variation in this parameter.
2) Density-dependence and public-information could be accounted for in future versions.
3) Since many Hawaiian forest bird species may start breeding in their first-year post-juvenile (Woodworth & Pratt 2009, Table 8.2), 1-year old birds are regarded as adults.

---

**m.natal**

**Definition:** The mean natal dispersal distance in km.

**Value:** $\in \mathbb{R}_0^+$ (0 and positive values)

**Ex:** $m.natal = 0.3$

**Note:**
1) We use random draws from a log-normal distribution ($X$) to calculate natal dispersal distances, with location and scale parameters ($\mu$ and $\sigma$) chosen such as $E(X) = m.natal$ and $SD(X) = SD.natal$ using the formulas: $\mu = \ln \left( \frac{m.natal^2}{\sqrt{m.natal^2 + SD.natal^2}} \right)$ and $\sigma = \sqrt{\ln \left( 1 + \frac{SD.natal^2}{m.natal^2} \right)}$.

2) Current version of *mamo* does not allow spatial variation in this parameter.

---

**SD.natal**

**Definition:** The standard deviation of natal dispersal distance in km.

**Value:** $\in \mathbb{R}_0^+$ (0 and positive values)

**Ex:** $SD.natal = 0.3$

**Note:**
1) We use random draws from a log-normal distribution ($X$) to calculate natal dispersal distances, with location and scale parameters ($\mu$ and $\sigma$) chosen such as $E(X) = m.natal$ and $SD(X) = SD.natal$ using the formulas: $\mu = \ln \left( \frac{m.natal^2}{\sqrt{m.natal^2 + SD.natal^2}} \right)$ and $\sigma = \sqrt{\ln \left( 1 + \frac{SD.natal^2}{m.natal^2} \right)}$.

2) Current version of *mamo* does not allow spatial variation in this parameter.

---

**psi.DD**

**Definition:** Coefficient affecting juvenile dispersal rates due to density-dependence. Mean and standard deviation of natal dispersal distance are multiplied by $psi.DD$ when local density is superior to $K.b$. 
Value: $[1, \infty)$
Ex: $psi.DD = 1$ (no effect)
Note: Must be $\geq 1$, but reasonably small values should be used (e.g., well below 10). For example, $psi.DD = 1.5$ means $m.natal$ is multiplied by 1.5.

2.1.8 Other options variables

<table>
<thead>
<tr>
<th>add.cline</th>
</tr>
</thead>
</table>

**Definition:** Logical: should a sigmoid curve (cline) be fitted to density values along the elevational gradient?

**Value:** TRUE or FALSE.

**Ex:** add.cline = FALSE

**Note:**

1) Calling the elevational gradient $grad$, the cline is fitted using the formula:

$$a + \frac{b-a}{1 + e^{-K \cdot (grad - c)}}$$

where the constants a, b, K and c are obtained using the *nls* function in R.

2) The algorithm may fail to estimate the parameters of the cline if density is not sigmoidal, but can also be unpredictable when the pattern appears to be a sigmoid. To prevent *mamo* from executing an error action, we use the warnonly = TRUE option of the *nls* function (fitting the sigmoid), which will return a warning message in case of convergence failure. However, even if convergence has not been reached, *nls* will provide an estimate for the cline parameters that will be automatically added to the *mamo* plot (see chapter 2.2) if add.cline = TRUE. More flexible algorithms, such as GAM (generalized additive model), may be implemented in future versions.

2.2 Running *mamo*

2.2.1 First use
Initially, running the function *mamo* can be decomposed into a 7-step process. In subsequent runs, only three steps will be necessary.

1) Open a R workspace, e.g. by double-clicking on the icon of the R Graphical User Interface (RGui).

2) Install the following R packages: *truncnorm*, *compiler*, *pastecs*, *lme4*, *plotrix*, *rsm*, *ade4*, *ggplot2* and *msm* by copying and pasting the following code (in green). Some of these packages are not necessary to run *mamo* per se, but they will be useful for additional use of the MAMO software.

```r
install.packages("truncnorm")
install.packages("compiler")
install.packages("pastecs")
install.packages("lme4")
install.packages("plotrix")
install.packages("rsm")
install.packages("ade4")
install.packages("ggplot2")
install.packages("msm")
```
3) Tell R where to find the source code corresponding to MAMO. We created a folder called 'MAMO' containing all the source code and some additional elements that will be discussed later. In our case, 'MAMO' is in a folder called 'Programs' that we created on the C hard drive of the computer (you would have to modify the pathway if you placed the MAMO file in a different folder).

```r
# Location of the source files
setwd("C:/Programs/MAMO")
```

4) Read the R code that will load the required R libraries.

```r
# load libraries
source("m2_libraries.r")
```

5) Read the R code that will load the required data sets.

```r
# load data sets
source("m3_data.r")
```

6) Read the R code corresponding to the `mamo` function

```r
# load the mamo function
source("m4_mamo.r")
```

7) Run mamo

```r
# run an example of MAMO
mamo.ex = mamo(
    # Spatial structure
    nr = 10, nc = 2, grad = c(1900, 1000), unit = 1,
    # Time frame
    T = 60, Tm = 5, t.b = 242, f.nb.1 = 0.5, min.fledg = 100, peak.fledg = (2/3), SD.fledg = 0,
    # Initial conditions
    init.1 = 300, init.2 = 300,
    # Survival (ad = annual, juv = from fledging to breeding age)
    s.ad = 0.729, rat.s = 0, s.juv = (0.729/2),
    # Reproduction and habitat quality
    fec = 3, fec.1 = 3, rat.f = 0, K.b = 600, thr.DD = 300, K.nb.1 = K.nb.1.2004, K.nb.2 = K.nb.2, reproduction.malaria = "simple",
    # Malaria parameters (daily except Sm.ac)
    alpha.b = alpha.b, alpha.nb.1 = alpha.nb.1, alpha.nb.2 = alpha.nb.2, Sm.ac = 0.13,
    # Movements
    gamma.mov = 0.541, calc.gamma.d = "fast.risky", n.sim.disp = 10000, R.ter = 0.0234,
    # Other options
    fidelity.ad = 0.95, m.natal = 0.3, SD.natal = 0.3, psi.DD = 1,
    add.cline = TRUE)
```
Details of the simulation are stored in the R object `mamo.ex`. In particular, `mamo.ex$np` contains the simulated vector of population size (the number of pairs in a square patch of side = unit km) along the elevational gradient measured by the vector `mamo.ex$grad` (elevation in km). We will get back on `mamo` output in more detail later. For now, we note that `mamo` automatically produces a figure plotting `np` as a function of `grad` (Fig. 2.2.1-1; note that figures related to dispersal are temporarily displayed during the `mamo` run, but they are not of direct interest to the user and can be ignored). Population size at each elevation is represented by a circle of one of the following colors: purple when the growth rate \( GR = \frac{N_t}{N_{t-1}} \) as averaged over the last three years of simulation, is \( \geq 1 \), blue when \( 0.9 \leq GR < 1 \), orange when \( 0.8 \leq GR < 0.9 \), and red when \( GR < 0.8 \) or \( GR = NA \). The latter happens for instance when population size during any of the last three years is zero. If the populations we simulated were sampled at or near equilibrium, and are significantly above zero, we generally expect a mixture of purple and blue points (see Fig 2.2.1-1). Finally, the carrying capacity in the absence of malaria (parameter \( K.b \)) is shown as a dashed black line. Note that if you run the same piece of code again, a slightly different figure will be produced, due to demographic stochasticity.

**Fig. 2.2.1-1.** Result of `i`iwi population simulation along an elevation gradient using `mamo`.

### 2.2.2 Subsequent use

Now that the required R packages have been installed, only 3 steps are necessary to run the function `mamo`.

1) Open a R workspace, e.g. by double-clicking on the icon of the R Graphical User Interface (RGui).

2) Load all the necessary source code, including libraries, data sets, and all MAMO functions. The simplest way to do this is opening the MAMO file called `m1_SCRIPT.r` (hereafter called SCRIPT file) in a text editor such as Notepad++, and copy and paste in R the code at the beginning of the file, called BLOCK 1, starting with `setwd("C:/Programs/MAMO")` and ending with `source("m14_f.data.community.r")`. Remember to adjust working directory if different.

The first two steps will need to be repeated every time a new MAMO session is conducted, no matter what component of the program is performed (calibration, analyzing outputs, etc).

3) Run `mamo`
At this point R is ready to run the previous example of MAMO, whose code can be found in the
BLOCK 2 of the SCRIPT file.

The *mamo* parameter values used in this example were chosen to replicate the current
distribution of IIWI along the elevational gradient along the Hamakua coast. It is therefore
possible to visually estimate the fit
between observed and simulated data by
plotting the observed data points using
black crosses with the following code
(please see the file called ‘m3_data.r’ for
details regarding the IIWI data,
y.obs.IIWI.1). As you can see in Fig.
2.2.2-1, the simulation run does a good
job of replicating the observed
distribution.

points(seq(1.9, 1.0, length.out = 10),
(y.obs.IIWI.1*100), pch = 3, col =
"black", cex = 1, lwd = 4)

You can change a single parameter of the
model to see how it affects the prediction.
For instance, consider changing *fec.1* from 3
to 0, which means that first-year birds do not
produce any young. We reproduce the code
of BLOCK 2 (below), with the change in bold
and colored orange. As you can see in Fig.
2.2.2-2 (and hopefully, in your R console!),
this time the fit is not quite as good. As one
would expect, there are fewer birds
predicted using this new parameter value.

```
# BLOCK 2
# run an example of MAMO

mamo.ex = mamo(
  # Spatial structure
  nr = 10, nc = 2, grad = c(1900, 1000), unit = 1,
  # Time frame
  T = 60, Tm = 5, t.b = 242, f.nb.1 = 0.5,
  min.fledg = 100, peak.fledg = (2/3),
  SD.fledg = 0,
  # Initial conditions
  init.1 = 300, init.2 = 300,
  # Survival (ad = annual, juv = from fledging
to breeding age)
  s.ad = 0.729, rat.s = 0, s.juv = (0.729/2),
```

---

**Fig. 2.2.2-1.** *’I‘iwi population simulation using mamo along an elevation gradient with corresponding count data (crosses).*

**Fig. 2.2.2-2.** *’I‘iwi population simulation using mamo with reduced fecundity of 1-yr old birds.*
# Reproduction and habitat quality

fec = 3, fec.1 = 0, rat.f = 0, K.b = 600, thr.DD = 300, K.nb.1 = K.nb.1.2004, K.nb.2 = K.nb.2, reproduction.malaria = "simple",

# Malaria parameters (daily except Sm.ac)

alpha.b = alpha.b, alpha.nb.1 = alpha.nb.1, alpha.nb.2 = alpha.nb.2, Sm.ac = 0.13,

# Movements

gamma.mov = 0.541, calc.gamma.d = "fast.risky", n.sim.disp = 10000, R.ter = 0.0234, fidelity.ad = 0.95, m.natal = 0.3, SD.natal = 0.3, psi.DD = 1,

# Other options

add.cline = TRUE)

# see output

mamo.ex

# Add real data points for comparison

points(seq(1.9, 1.0, length.out = 10), (y.obs.IIWI.1*100), pch = 3, col = "black", cex = 1, lwd = 4)

Finally, here is a last example where a single parameter has been changed, from T = 60 to T = 10. As you can see in Fig. 2.2.2-3, the populations in the upper sites are already at or near equilibrium, but the populations in the lower ranges, the most affected by malaria, are not and are still decreasing to their actual equilibrium (see Fig. 2.2.2-1 for equilibrium value).

### 2.3 mamo output

As a rule, the input variable and their values are returned by *mamo*. This helps the user keep track of the input values that produced a given result. For some variables, the input value is returned without any modification.

This includes *nr, nc, unit, T, Tm, reproduction.malaria, Sm.ac, gamma.mov, calc.gamma.d, n.sim.disp, R.ter, fidelity.ad, m.natal, SD.natal, psi.DD*, and *add.cline*.

For the rest of the arguments, the actual output is generally modified from a number or a vector into a matrix (see chapter 2.1.1 for an explanation). The arguments that can vary spatially fall into this category.

This includes *t.b, t.nb, t.nb.2, min.fledg, peak.fledg, SD.fledg, init.1, init.2, s.ad, rat.s, s.juv, fec, fec.1, rat.f, K.b, thr.DD, K.nb.1, K.nb.2, alpha.b, alpha.nb.1, alpha.nb.2*.
The argument *grad* is transformed into a vector of length *nr* using the formula `seq(grad[1], grad[2], length = nr) / 1000`. For instance, a gradient entered as argument as `grad = c(1900, 1000)` in meters will be returned as the following vector: (1.9, 1.8, 1.7, 1.6, 1.5, 1.4, 1.3, 1.2, 1.1, 1.0) in km.

Last, the following set of variables are new:

- **s.ad.d** and **s.juv.d** are the daily survival rates for adult and juveniles; **s.ad.d** is calculated over the entire year (i.e., `s.ad.d = s.ad ^ (1/365)`), while **s.juv.d** is calculated over a period of `(365 - peak.fledg × t.b)` days.

- **K.nb.1.high**, **K.nb.1.mid**, **K.nb.1.low**, **K.nb.2.high**, **K.nb.2.mid**, and **K.nb.2.low** correspond to the value of K.nb.1 or K.nb.2 at high (1800 m), mid (1500m) and low (1200 m) elevation, respectively. Note that these values are returned only if `grad[1] ≥ 1.9` and `grad[nr] ≤ 1.1`, otherwise, NA is returned.

- **alpha.b.low**, **alpha.nb.1.low**, and **alpha.nb.2.low**, are the corresponding value of the daily probability of malaria infection of a susceptible e-bird (‘alpha’) at the low (1,200 m) elevation band during the breeding season, first period of the non-breeding season, and second period of the non-breeding season, respectively. Note that these values are returned only if `grad[1] ≥ 1.9` and `grad[nr] ≤ 1.1`. Otherwise, NA is returned.

Used for debugging purpose, the parameter **gamma.d.breed** is the estimate of the hidden parameter **gamma.d** for the (nr×nc)th patch. Hence **gamma.d.breed** is a negative exponential distribution parameter estimated in order to distribute `fraction.disp` leaving the (nr×nc)th patch into the remaining nr×nc-1 patches. A second parameter, **test.disp.breed**, checks that the fraction of breeders that left one patch after breeding dispersal is about equal to the value of the hidden variable **fraction.disp**; **test.disp.breed** therefore tests the ability of the negative exponential with parameter **gamma.d** to shuffle the right amount of dispersers into neighboring patches. **It is essential that users check that test.disp.breed has a value close to zero (typically ~ 10^-9-10^-8) if calc.gamma.d = "fast.risky" has been chosen.** If any **test.disp.breed** value in the simulation set is larger than ~ 10^-3, we advise re-running the analyses using calc.gamma.d = "slow.robust".

The variables **disp.breed** and **disp.natal** give the patch-specific transition probability matrices based on natal and breeding dispersal distances, respectively, while accounting for patch and grid dimensions and resource distribution; for instance, `disp.breed[[1]][1]` is the probability for an adult of patch 1 to remain in its former breeding patch next year, `disp.breed[[1]][3]` is the probability that it instead breeds in patch 3, while `disp.breed[[4]][1]` is the probability that an adult from patch 4 disperses into patch 1. The variable **disp.natal.DD** gives the (higher) natal dispersal probabilities that apply when `psi.DD > 1` and the breeding population is above `thr.DD`. For 'migratory' species, the variables **disp.nb.1** and **disp.nb.2** give the patch-specific transition probability matrices based on the 'migratory propensity' parameter **gamma.mov**, patch and grid dimensions, and the resource distribution during the non-breeding seasons; for instance, `disp.nb.1[[1]][2]` is the probability that a breeding adult or juvenile of patch 1 spends the first part of the non-breeding season (nb.1) in patch 2.

The two variables **mal.y** and **mal.a** are only valuable for internal routines and could be removed as outputs from future **mamo** versions.
The next set of variables, namely $n.1$, $n.ad$, $n.pairs$ and $n.juv$, are arrays of dimension $nr$, $nc$, and $T$, containing the number of first-year, adults, pairs and juveniles at the beginning (all except $n.juv$) or end ($n.juv$) of the breeding season for each year from 1 to $T$, respectively. For instance, $n.pairs[][,,10] = n.1[][,,10] + n.ad[][,,10]$ gives the number of females (or pairs) at the beginning of the 10th breeding season in each patch of the spatial grid; $n.pairs[1,1,20]$, which can also be called by $n.pairs[][,,20][1]$, is the number of pairs at $T = 20$ in the first patch.

To obtain the elevation-specific average number of pairs at the end of the simulation (variable $np$, the average for a single patch), the number of breeding pairs are averaged over the last three years of simulation and over the $nc$ columns of the grid, in order to attenuate the effect of demographic stochasticity across space and time; $np$ values obtained at an elevation of 1800 (1750-1850), 1500 and 1200 m are called $np.high$, $np.mid$ and $np.low$, respectively. The variables $r.hm$ and $r.ml$ are simply the ratio between $np.high$ and $np.mid$, or $np.mid$ and $np.low$, respectively. The total number of pairs in the final population (all patches) is calculated as $np.metapop = nc \times \sum_{k=1}^{nr} np_k$.

For illustration purposes, we fit a sigmoid curve to $np$ values along the elevational gradient $grad$ using the formula: $a + \frac{b-a}{1 + e^{-K \cdot (grad - c)}}$, where the constants $a$, $b$, $K$ and $c$ were obtained using the nls function in R. The output variables cline.2, cline.5, and cline.8 are the values of $grad$ for which $np$, as modelled by the sigmoid, is 20%, 50% and 80% of its maximum, respectively; note that cline.5 is the center c of the cline (inflection point).

As we previously mentioned for the plot produced by a $mamo$ run, we calculate for each patch the growth rate ($\Delta R = \frac{N_t}{N_{t-1}}$), averaged over the last three years of simulation. The growth rate is next averaged across patches in the same elevation to produce the output variable $gr$; the variables $gr.high$, $gr.mid$, and $gr.low$ are simply $gr$ values at 1800, 1500 and 1200 m, respectively. Note that NA values can be obtained (e.g., if a denominator value is 0).

Finally, $m.elev$ is the mean elevation in the gradient: $m.elev = \frac{\sum_{i=1}^{nr} grad_i np}{\sum_{i=1}^{nr} np}$, while $m.elev.np$, $m.elev.K.nb.1$, $m.elev.K.nb.2$, $m.elev.gr$, $m.elev.alpha.b$, $m.elev.alpha.nb.1$, and $m.elev.alpha.nb.2$ are weighted average measures of elevation along the gradient, with weights $np$, $K.nb.1$, $K.nb.2$, $gr$, $alpha.b$, $alpha.nb.1$ and $alpha.nb.2$, respectively. For instance, $m.elev.np = \frac{\sum_{i=1}^{nr} grad_i np}{\sum_{i=1}^{nr} np}$ and $m.elev.gr = \frac{\sum_{i=1}^{nr} grad_i gr}{\sum_{i=1}^{nr} gr}$. Weighted averages indicate the location of the center of mass; for instance, in presence of malaria, we expect $m.elev.np > m.elev$ because more pairs will be present at high (refuge) versus low elevation.

**Chapter 3: CALIBRATING MAMO**

**3.1 The $f.calibr$ function**

Calibration involves determining a set of $mamo$ parameters values capable of replicating the current pattern of distribution of the study species along an elevational gradient. This is important for obtaining meaningful predictions when, for instance, we want to predict the impact of a management action, or future climatic conditions.
To achieve this, we introduce a new function called \textit{f.calibr}. Essentially, \textit{f.calibr} calls and runs \textit{mamo} as many times as needed to explore a desired range of parameter combinations. The results are then stored in a folder created by the user. The argument \textit{output.dir} of the function \textit{f.calibr} is used to indicate the location of the folder.

\textbf{Ex:} \texttt{output.dir = "C:/Programs/MAMO/\textit{\textbf{CALIBRATION/run/IIWI.1_1}"}}

Raw calibration results are stored in this folder in two different ways. First, a subset of \textit{mamo} results are stored in a text file called \textit{t.sim.txt}. Each row will contain the results of a single simulation run. \textbf{Importantly, in the current version of MAMO, an empty file called \textit{t.sim.txt} must be created by the user and put into the destination folder (\textit{output.dir}) before the calibration starts.} At the end of each calibration run, \textit{t.sim.txt} will be called in and results will be added. Such an empty file is available in the folder C:/Programs/MAMO/\textit{\textbf{CALIBRATION/run/aaa_empty table}}. Hence, the simplest (and recommended) way to create the calibration output folder is to copy the folder 'aaa_empty table', paste it, and rename it. In our example, since we want to name the output folder 'IIWI.1_1' (as \textit{output.dir = "C:/Programs/MAMO/\textit{\textbf{CALIBRATION/run/IIWI.1_1}"}), we would change the folder name 'aaa_empty table - Copy' to 'IIWI.1_1'.

Second, an R file containing the complete \textit{mamo} output will be produced for each calibration run, named s1.1.rdata for the first, s2.1.rdata for the second, etc. The \textit{f.calibr} argument \textit{n.sim} allows the user to run each parameter combination more than once, in order to test the effect of demographic stochasticity (e.g., \textit{n.sim} = 2). In that case, the files s1.2.rdata and s2.2.rdata also will be produced. Finally, another R file is produced synthesizing \textit{mamo} outputs for the \textit{n.sim} calibration run of each parameter combination. In our example, they would be called s1.rdata, and s2.rdata, respectively. Like for the text file, only a subset of \textit{mamo} output is stored in this latter R file. Double-clicking on any R file opens the R program. The results can be accessed by typing \texttt{x} in the console.

Another critical argument of \textit{f.calibr} is called \textit{d}, a data set established beforehand which gives \textit{f.calibr} important information regarding the parameter values to be explored. In our example, \textit{d} = \texttt{read.table("C:/Programs/MAMO/\textit{\textbf{CALIBRATION/Starting parameters/param_calib.IIWI.1.txt}", header = T, sep = ",", dec = ".").} This apparently complex formula simply tells \textit{f.calibr} to read the text file called 'param_calib.IIWI.1.txt' located in the folder 'Starting parameters', with the added indications that the text file contains header, decimals are "," as opposed to ",", etc.

The file param_calib.IIWI.1.txt contains the input value of parameters meant to be fixed across the calibration runs, namely \textit{t.b, f.nb.1, min.fledg, and peak.fledg}. Of course, the assumption that these parameters are known without uncertainty could be relaxed in future versions of MAMO.

The file param_calib.IIWI.1.txt also contains the range of parameter values that we want to explore for another set of 13 variables such as \textit{rat.s} (\textit{rat.s} measures the extra mortality of breeding females due to rat predation). Specifically, the table contains the minimum and maximum parameter values that the user considers biologically likely. Arguments specific to \textit{f.calibr} are associated with each of these 13 variables, called \textit{n.rat.s for rat.s, n.s.ad for s.ad} and so on. This specific argument tells \textit{f.calibr} how many values of each parameter we want to examine during calibration. For instance, if \textit{n.rat.s} = 1, only the minimum value of \textit{rat.s} will be
used; if n.rat.s = 2, both the minimum and maximum values of \textit{rat.s} will be used. Beyond 2, a regular sequence of values from min to max is constructed; e.g., if n.rat.s = 3, the minimum, maximum and average (of min and max) values of \textit{rat.s} will be used.

The set of 13 variables involved in the calibration process can be separated into three groups. For a first group of 7, namely \textit{rat.s}, \textit{rat.f}, \textit{K.b}, \textit{R.ter}, \textit{fidelity.ad}, \textit{m.natal}, and \textit{psi.DD}, the calibration process is identical to what we just described for \textit{rat.s} (called Proc.1).

For \textit{K.nb.1}, the default argument of \textit{f.calibr} is \texttt{K.nb.1 = list(K.nb.1.2003, K.nb.1.2004, K.nb.1.avg)}. If n.K.nb.1 = 3, all three candidate values for \textit{K.nb.1}, namely K.nb.1.2003, K.nb.1.2004 and K.nb.1.avg will be examined in turn. Instead, if n.K.nb.1 = 2, the minimum and maximum values in the file 'param_calib.IIWI.1.txt' will be used. No other option is allowed.

For the final set of five variables in the third group, namely \textit{s.ad}, \textit{fec}, \textit{fec.1}, \textit{Sm.ac}, and \textit{gamma.mov}, another specific \textit{f.calibr} parameter is associated with each of them, respectively called \textit{input.direct.s.ad}, \textit{input.direct.fec}, etc.... These 'input.direct' parameters are logical, i.e. they can take the value TRUE or FALSE. For instance, if \textit{input.direct.s.ad} = FALSE, then Proc.1 applies and the number of \textit{s.ad} values examined will depend on \textit{n.s.ad}. If \textit{input.direct.s.ad} = TRUE, however, the values examined are determined by yet another \textit{f.calibr} parameter, called \textit{s.ad.direct} in this case (for \textit{fec}, the corresponding parameter is \textit{fec.direct}, etc.). The reason for adding this level of complexity is that for these variables, a regular sequence of values between min and max may not be appropriate, due to non-linear effects for instance (e.g., \textit{gamma.mov}).

The majority of remaining arguments are identical to the ones described for \textit{mamo}, with the following exceptions:

- \textit{sp} is the species considered; so far, it can be any of the eight native forest bird species that breed at Hakalau National Wildlife Refuge in Hawaii: the Hawai‘i ‘elepaio (\textit{Chasiempis s. sandwichensis}) is a monarch flycatcher (Monarchidae), and the ‘ōma‘o (\textit{Myadestes obscurus}) is a thrush (Turdidae); the remaining six species are Hawaiian honeycreepers: the ‘apapane (\textit{Himatione sanguinea}), ‘ī‘īwi, Hawai‘i ‘amakihi (\textit{Chlorodrepanis virens}), ‘akiapōlā‘au, Hawai‘i ʻākea, and Hawai‘i creeper. Corresponding acronyms for \textit{sp} are "ELEP", "OMAO", "APAP", "IIWI", "HAAM", "AKIP", "AKEP" and "HCRE", respectively.

- \textit{y.obs} is the observed vector of species distribution along the considered elevational gradient (as defined by the argument \textit{grad}), that is taken from the data file called 'm3_data.r'. It will be used to choose the set of calibration runs that best predict the observed data.

- \textit{paired.s.ad.fec} is logical (TRUE or FALSE); if FALSE, \textit{n.s.ad} × \textit{n.fec} combinations of parameters are run for these two parameters (i.e., all possible combinations); if TRUE, only paired values are run. For instance, if \textit{input.direct.s.ad} = \textit{input.direct.fec} = TRUE and \textit{n.s.ad} = \textit{n.fec} = 2, the only combinations allowed will be \texttt{s.ad.direct[1]-fec.direct[1]} and \texttt{s.ad.direct[2]-fec.direct[2]}. This is useful if we want the calibration run to be shorter, assuming that the maximum annual fecundity (\textit{fec}) and adult survival (\textit{s.ad}) are linked in avian species, and that only certain combinations are reasonable (see the 'IIWI paper' Appendix S4.2. for details).

- \textit{alpha.1} is a data set described in the data file; it is the daily probability of infection of a susceptible e-bird staying in the same patch during the whole year (applicable to non-migratory species).
- **design** and **batch** are two arguments required by `simul_mamo`, an ancillary function that 'transmits the information' between `f.calibr` and `mamo`. In the current version of MAMO, use of default values for **design** and **batch** ("simple" and 1, respectively) is required.

### 3.2 Running `f.calibr`

The code of BLOCK 3 of the SCRIPT file is reproduced below. **It will perform the calibration step of the 'IIWI paper' once we change the code of the first row from `run_f.calibr = FALSE` to `run_f.calibr = TRUE`.** This line of code is here to ensure that the user will not inadvertently run the calibration again if she/he does not intend to, which would automatically erase the previous results. **Importantly, the user has to wait until all simulations are complete before opening the `t.sim.txt` file, otherwise calibration will fail.** Changes in the sleep mode of the computer may be needed as the process took us 31 hours and 9 minutes on a DELL LATITUDE E6230 with a 2.8 GHz Intel Core 3rd Generation i5-3360M Processor. You can monitor the progress of the calibration by looking into the IIWI_1 folder you created, as .R files start to be created and accumulate from `s1.rdata` onwards. In this case, the calibration should end after the file `s5184.rdata` is created. Your R window should be active as well; a total of 5184 Figures will be produced throughout the calibration process (as expected since ultimately, we are conducting `mamo` runs), although they will not be saved.

```r
# BLOCK 3
# CALIBRATE MAMO FOR A SINGLE SPECIES: THE ALTITUDINAL MIGRANT IIWI ('IIWI paper')
run_f.calibr = FALSE # CHANGE TO run_f.calibr = TRUE to launch the calibration

#---
if(run_f.calibr == TRUE) {

f.calibr(

  # species
  sp = "IIWI", output.dir = "C:/Programs/MAMO/CALIBRATION/run/IIWI.1_1",
  y.obs = y.obs.IIWI.1,
  d = read.table("C:/Programs/MAMO/CALIBRATION/Starting parameters/param_calib.IIWI.1.txt", header = T, sep = "\t", dec = "."),

  # Spatial structure
  nr = 10, nc = 2, grad = c(1900, 1000), unit = 1,

  # Time frame
  T = 60, Tm = 5, SD.fledg = 0,

  # Survival (ad = annual, juv = from fledging to breeding age)
  n.s.ad = 3, input.direct.s.ad = TRUE, s.ad.direct = c(0.729, 0.78, 0.877), n.rat.s = 1,

  # Reproduction and habitat quality
  n.fec = 3, input.direct.fec = TRUE, fec.direct = c(3, 2.444, 1.5), n.fec.1 = 3, input.direct.fec.1 = TRUE, fec.1.direct = c(3, 2.444, 1.5),

)
reproduction.malaria = "simple",

# Malaria parameters (daily except Sm.ac)
alpha.b = alpha.b, alpha.nb.1 = alpha.nb.1, alpha.nb.2 = alpha.nb.2, alpha.1 = alpha.1,
n.Sm.ac = 3, input.direct.Sm.ac = TRUE,
Sm.ac.direct = c(0.02, 0.07, 0.13),

# Movements
n.gamma.mov = 4, input.direct.gamma.mov = TRUE, gamma.mov.direct = c(-10, 0.159, 0.541, 10), calc.gamma.d = "fast.risky",
n.sim.disp = 10000, n.R.ter = 1, n.fidelity.ad = 2, n.m.natal = 2, n.psi.DD = 2,

# Other options
add.cline = FALSE,

# Simulations
n.sim = 1, design = "simple", batch = 1)
}

3.3 The 'demographic envelop'

3.3.1 The function f.envp.single
Once the calibration runs are completed, we need to identify the ones that best predict the observed data (the so-called 'demographic envelop'). This is the role of the function f.envp.single.

The function f.envp.single has seven arguments, and the majority have previously been described for mamo or f.calibr, with the following exceptions:

- output.dir this time describes not where the results of the calibration will be stored, but where they are stored.

- col is the color used to plot the observed data (represented by crosses); simulated data is always shown in pink.

- n.envp is the number of best runs the user wants to include in the envelop. Runs are ranked using a least-squares approach, wherein \( fit \propto -\sum_{i=1}^{nr} (obs_i - sim_i)^2 \).

Running the function in the case of the 'IIWI paper' can be done as follows (code also found in BLOCK 4 of the SCRIPT file)(ensure correct working directory)

IIWI.1_1.calibr = f.envp.single(
sp = "IIWI",
output.dir = "C:/Programs/MAMO/CALIBRATION/run/IIWI.1_1",
y.obs = y.obs.IIWI.1, n.envp = 10, col = "blue",
)
d = read.table("C:/Programs/MAMO/CALIBRATION/Starting parameters/param_calib.IIWI.1.txt", header = T, sep = "\", dec = ".")

Fig. 3.3. Simulation results that identify the 10 best combination of demographic parameters matching the observed elevation distribution (crosses) with population estimates (pink squares).

A Figure is automatically produced once we execute the function (Fig. 3.3.1-1). Note that a slightly different figure should be obtained if you run the calibration step from scratch, due to demographic stochasticity. Furthermore, the actual envelop will probably contain a different set of runs. This is to be expected.

Of course, if you are increasing the number of runs included in the 'demographic envelop', the envelop's variance will increase. This is shown in Figure 3.3.1-2, which was obtained by changing the argument `n.envp` from 10 to 100.
3.3.2 Outputs of \texttt{f.envp.single}

In addition to producing a figure that can help us visualize whether the calibration step produced a reasonable fit with observed data (e.g., Fig. 3.3.1-1), the function \texttt{f.envp.single} returns a list of four variables stored in the object we created when running the function which, in this case, we called IIWI.1_1.calibr (see above). Normally the user will not have to deal directly with these outputs, so we will only present them briefly here.

1) The variable \texttt{d.sim} essentially corresponds to the calibration file called \texttt{t.sim.txt}. It can be seen in R by using the \texttt{edit} function using the code:
\begin{verbatim}
edit(IIWI.1_1.calibr$d.sim)
\end{verbatim}

Normally, the data set should contain 5184 rows if the code BLOCKS 1-4 has been used without modifications.

2) The variable \texttt{envp} contains the \texttt{n.envp} rows of \texttt{d.sim} that best predicted the observed data:
\begin{verbatim}
edit(IIWI.1_1.calibr$envp)
\end{verbatim}

3) The variable \texttt{stat.envp} contains information on the set of 13 variables that can be subjected to calibration:
\begin{verbatim}
edit(IIWI.1_1.calibr$stat.envp)
\end{verbatim}

For each of the 13 variables, five statistics are reported:
\begin{itemize}
\item[i)] mean.envp is the mean value of the parameter in the envelop
\item[ii)] sd.envp is the standard deviation of the parameter in the envelop
\item[iii)] min.envp is the minimum value of the parameter in the envelop
\item[iv)] max.envp is the maximum value of the parameter in the envelop
\item[v)] exp.mean is the expected average value of the parameter in the whole calibration run
\end{itemize}

4) The output variable \texttt{d} is the modification of the input variable \texttt{d} accounting for \texttt{stat.envp}. Specifically, for each of the 13 variables subjected to calibration, if mean.envp \(\geq\) exp.mean, it implies that best-fitting runs tend to have a relatively high value for this parameter. After the first round, if we are interested in running further calibrations in order to more closely match reality, we would be tempted to discard the low-end values of this parameter. We therefore modify \texttt{d} such that the minimum value of the parameter corresponds to \texttt{exp.mean}, and we leave the maximum value unchanged. Conversely, if mean.envp < exp.mean, we modify \texttt{d} such that the maximum value for the parameter corresponds to \texttt{exp.mean}, and the minimum value is unchanged. The modified data set \texttt{d} can then be used as input for the function \texttt{f.calibr} to run yet another round of calibration.

Fig. 3.3.1-2. Demographic envelop simulation results that include the top 100 runs (as opposed to 10; compare with Fig. 3.3.1-1).
In this example, we are not interested in running a second round of calibration, so we can create the final 'demographic envelop' object called envp.IIWI.1_1 using the code:
\[ \text{envp.IIWI.1_1} = \text{IIWI.1_1.calibr}\text{\$envp}. \]

### Chapter 4: Simulation Study

#### 4.1 The f.run function

Now that we have a set of parameter conditions capable of replicating the current pattern of IIWI distribution (our 'demographic envelop'), we can start asking questions concerning the impact of climate change or potential management actions. This is the role of the function \texttt{f.run}, to run a series of simulations covering the full spectrum of scenarios that we want to investigate while accounting for parameter uncertainty \textit{via} the 'demographic envelop'.

The \texttt{f.run} function is akin to the \texttt{f.calibr} function. Both call \texttt{mamo} repeatedly via the ancillary \texttt{simul_mamo} function, storing the results in a similar way: 1) a subset of \texttt{mamo} results are stored in a text file called \texttt{t.sim.txt} located in the \texttt{output.dir} folder created by the user; the simplest way to create the output folder is to copy the folder named 'aaa_empty table' located in the RUN folder of MAMO, paste it in the same folder, and rename it as necessary; make sure the code is changed, if necessary, to reflect directory and file name. This folder contains the required empty \texttt{t.sim.txt} file; 2) an \texttt{R} file containing the complete \texttt{mamo} output will be produced for each run, named \texttt{s1.1.rdata} for the first, \texttt{s2.1.rdata} for the second, etc. The argument \texttt{n.sim} of \texttt{f.run} allows the user to run each parameter combination more than once, in order to test the effect of demographic stochasticity (e.g., \texttt{n.sim} = 2). In that case, the files \texttt{s1.2.rdata}, \texttt{s2.2.rdata}, etc. will also be produced. Finally, the function will produce another \texttt{R} file that synthesizes the \texttt{mamo} outputs for the \texttt{n.sim} runs of each parameter combination. In our example, they would be called \texttt{s1.rdata}, and \texttt{s2.rdata}, respectively. Similar to the text file, only a subset of \texttt{mamo} output are stored in this latter \texttt{R} file. Double-clicking on any \texttt{R} file opens the \texttt{R} program. The results can be accessed by typing \texttt{x} in the console.

Unlike \texttt{f.calibr}, however, \texttt{f.run} will also yield a \textit{de novo} text file called \texttt{factors.txt} containing a number of variables characterizing the scenarios investigated for each run. In the current version of MAMO, these variables are limited to the following:

1) 'RISK' for malaria transmission risk; in the current version of MAMO, five scenarios are investigated when the argument of \texttt{f.run} calls \texttt{n.RISK} = 5. Actual transmission risk is expected to increase from \texttt{RISK} = 1 to 5, but we cannot exclude situations where this actually would not be the case (see below for details):
   i) \texttt{RISK} = 1: malaria transmission risk is zero all year round at all elevations; simulate pre-malaria conditions.
   ii) \texttt{RISK} = 2: malaria transmission risk corresponds to the present climatic conditions, but it is partly alleviated by management aiming at reducing transmission risk; such management is described by the \texttt{f.run} argument called \texttt{mg.RISK}; \texttt{mg.RISK} is a vector describing the effect of malaria reduction at each elevation. For instance, assuming \texttt{grad} = c(1900, 1000) and \texttt{nr} = 10, \texttt{mg.RISK} will be a vector of 10 elements starting with the effect of management at 1,900 m. In our case, we want to simulate the effect of a 50% reduction of malaria transmission risk at elevations \geq 1,600 m. This is accomplished by choosing \texttt{mg.RISK} = \texttt{c(rep(0.5, 4), rep(1, 6))}. 

iii) RISK = 3: corresponds to RISK = 2 but with no management.
iv) RISK = 4: corresponds to future, not present, climatic conditions and management action like for RISK = 2
v) RISK = 5: corresponds to RISK = 4 but without management action.

Note that if you pick n.RISK = 3, only scenarios i) through iii) will be explored; if n.RISK = 2, only scenarios i) and ii), etc. In the current version of MAMO, it is not possible to choose any particular subset, or introduce a new scenario; more flexibility may be introduced in future versions.

2) 'AC' which stands for acute malaria mortality, represents the probability of dying from the first, so-called 'acute', malaria infection. While the value of the mamo parameter Sm.ac is determined by the calibration process (in fact, we have n.envp different Sm.ac estimates, which can be identical or not), we cannot exclude that the species will evolve towards greater malaria tolerance in the future. Accordingly, it is possible to test a number of alternative scenarios (n.AC), where the current estimate of Sm.ac is multiplied by a factor called evol.AC. For instance, if n.AC = 2 and evol.AC = c(2, 1), the first n.envp run will be conducted with the Sm.ac estimate multiplied by 2, while the next n.envp run will be conducted with the Sm.ac estimate multiplied by 1. Because Sm.ac is the probability of surviving acute malaria infection, evol.AC = 2 corresponds to our 'guess' for the future value (after evolution), while evol.AC = 1 corresponds to the current estimate, or a scenario with no evolution of malaria tolerance in the future (due to lack of suitable genetic variation for instance). Note that by ranking the values in evol.AC in decreasing order, as we did here, we ensure that malaria mortality risk (our factor 'AC') increases from AC = 1 to n.AC. This choice is important to remember for correct interpretation of AC values.

Function f.run uses each and every possible value in the 'demographic envelope' to account for the uncertainty in demographic estimates. For instance, if n.envp = 2 and Sm.ac (in the envelop) = c(0.07, 0.13), then four run will be conducted with Sm.ac = 0.14 and 0.26 first (corresponding to evol.AC = 2), followed by Sm.ac = 0.07 and 0.13 (corresponding to evol.AC = 1). Of course, different Sm.ac values traded off with different values of other demographic parameters to produce similar calibration results, so for each run, the appropriate 'envelop' value is used as well for these other parameters.

3) RAT.S and RAT.F are two columns of factors.txt that report effects of management actions used to reduce rat predation on breeding females and juveniles, respectively. In the current version of MAMO, we assumed that reducing rat predation would affect the mamo parameters rat.s and rat.f similarly so RAT.S always = RAT.F. The number of management actions concerning rat predation can be controlled by the parameter n.RAT. The actual management actions are indicated by mg.RAT. For instance, if we want to test two scenarios for a spatial grid characterized by grad = c(1900, 1000) and nr = 10, one scenario which is status quo and the other one where we reduce rat predation on adults and juveniles by 30% at elevations ≥ 1600 m, we can use a list of two vectors as follows:

mg.RAT = list( rep(1, 10), c(rep(0.3, 4), rep(1, 6)) )

In the status quo scenario, the 'demographic envelop' values for rat.s and rat.f will be multiplied by 1 at all 10 elevations, while in the second scenario, a 70% reduction will be applied for elevations ≥ 1,600 m. Note that when the 'demographic envelop' value for rat.s or rat.f is zero, the management action will have no effect. In building mg.RAT, we recommend ordering management actions from least (left) to most (right), so that RAT.S (and RAT.F) increase from
RAT.S = 1 to n.RAT. For instance, if we want to test a third scenario where rat predation is reduced by 80% at elevations ≥ 1,400 m, we would write:

```
mg.RAT = list( rep(1, 10), c(rep(0.3, 4), rep(1, 6)), c(rep(0.2, 6), rep(1, 4)) )
```

The vector rep(1, 10) would be associated with RAT.S = RAT.F = 1 in `factors.txt`, the vector c(rep(0.3, 4), rep(1, 6)) with RAT.S = RAT.F = 2, and the vector c(rep(0.2, 6), rep(1, 4)) with RAT.S = RAT.F = 3.

4) RES.1 and RES.2 are two columns of `factors.txt` reporting management actions aimed at increasing the resources available to altitudinal migrants during the first (K.nb.1) and second (K.nb.2) periods of the non-breeding season, respectively. Unlike RAT.S and RAT.F, a unique strategy can be applied to each season. Again, we recommend ordering the management actions from left (least) to right (most) so that RES.1 and RES.2 increase from RES.1 = 1 to n.K.NB.1 and from RES.2 to n.K.NB.2, respectively. For instance, if we want to test 3 management scenarios for nb.2 and no management action for nb.1, with a spatial grid characterized by grad = c(1900, 1000) and nr = 10, we can use the following values of `f.run` arguments:

```
n.K.NB.1 = 1
mg.K.NB.1 = rep(1, 10) # no management
n.K.NB.2 = 3
mg.K.NB.2 = list( rep(1, 10), c(rep(1.5, 3), rep(1, 7)), c(rep(2, 3), rep(1, 7)) )
```

Hence for nb.2, the second part of the non-breeding seasons, we have a status quo for scenario 1, resources will be multiplied by 1.5 at elevations ≥ 1,700 m for scenario 2, and resources will be multiplied by 2 at elevations ≥ 1,700 m for scenario 3.

5) ENVP and SIM, the last two columns of `factors.txt`, report the rank of the 'demographic envelop' (from 1 to n.envp, 1 being the parameter combination which produced the best fit with observed data) and the replicate number for each unique parameter combination (from 1 to n.sim). These data will be useful for conducting subsequent statistical analyses.

Most of the other arguments of `f.run` are shared with the functions described previously, so they will not be detailed here, with the following exceptions:

- The `envp` argument is the 'demographic envelop' object. In our ongoing example, `envp = envp.IIWI.1_1`.

- Currently, the `K.nb.1` argument need to use the default, i.e. `K.nb.1 = list(K.nb.1.2003, K.nb.1.2004, K.nb.1.avg)`

- We introduce here future (2100) malaria transmission risk variables, `alpha.b.2100`, `alpha.nb.1.2100`, `alpha.nb.2.2100`, and `alpha.1.2100`, that are equivalent counterparts of `alpha.b`, `alpha.nb.1`, `alpha.nb.2`, and `alpha.1`, respectively.

We are now ready to run the simulation study by using the following code (BLOCK 5 of the SCRIPT file reproduced below). Remember to change run_f.run from FALSE to TRUE otherwise the code will not be read (precaution against inadvertent launch of a run which would erase previously obtained results). As for the calibration step, remember to wait until completion of all the simulation before opening the `t.sim.txt` file, otherwise run will fail.
in the sleep mode of the computer may be needed as the process took us 3 hours and 29 minutes on a DELL LATITUDE E6230 with a 2.8 GHz Intel Core 3rd Generation i5-3360M Processor. You can monitor the progress of the simulation study by looking into the IIWI_1 folder you created within the RUN folder of MAMO, as .R files start to be created and accumulate from s1.1.rdata onwards. In this case, the study should end after the file factors.txt has been created. Your R window should be active as well during the study; a total of 900 figures will be produced throughout the study, although they will not be saved (n.RISK = 5 × n.AC = 3 × n.K.nb.2 = 3 × n.sim = 2 × n.envp = 10: the latter not an explicit f.run argument, but accessible to the function via the envp argument).

```r
# BLOCK 5
# Run management scenarios based on the 'demographic envelop' for the 'IIWI paper'
r_f.run = FALSE # CHANGE TO run_f.run = TRUE to launch the simulation study

#---
if(run_f.run == TRUE) {

IIWI.1_1.run = f.run(

# species-specific
sp = "IIWI",
envp = envp.IIWI.1_1,
output.dir = "C:/Programs/MAMO/RUN/IIWI.1_1",
y.obs = y.obs.IIWI.1,
d = read.table("C:/Programs/MAMO/CALIBRATION/Starting
parameters/param_calib.IIWI.1.txt", header = T, sep = "\\t", dec = "."),

# Spatial structure
nr = 10, nc = 2, grad = c(1900, 1000), unit = 1,
# Time frame
T = 60, Tm = 5, SD.fledg = 0,

# Survival
n.RAT = 1,
mg.RAT = rep(1, 10),

# Reproduction and habitat quality
K.nb.1 = list(K.nb.1.2003, K.nb.1.2004, K.nb.1.avg),
n.K.NB.1 = 1,
mg.K.NB.1 = rep(1, 10), # no management
K.nb.2 = K.nb.2,
n.K.NB.2 = 3,
mg.K.NB.2 = list( rep(1, 10), c(rep(1.5, 3), rep(1, 7)), c(rep(2, 3), rep(1, 7)) ),
reproduction.malaria = "simple",

# Malaria parameters (daily except Sm.ac)
n.RISK = 5, mg.RISK = rep(0.5, 10),
alpha.b = alpha.b, alpha.nb.1 = alpha.nb.1, alpha.nb.2 = alpha.nb.2, alpha.1 = alpha.1,
```

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alpha.b.2100 = alpha.b.2100, alpha.nb.1.2100 = alpha.nb.1.2100, alpha.nb.2.2100 = alpha.nb.2.2100, alpha.1.2100 = alpha.1.2100,

n.AC = 3, evol.AC = c(3, 2, 1),

# Movements
calc.gamma.d = "fast.risky",
n.sim.disp = 10000,

# Other options
add.cline = FALSE,

# Simulations
n.sim = 2, design = "simple", batch = 1
}
}

4.2 Analysis of the simulation study

In the following chapters, we will present a number of tools used to visualize and analyze the results. The different blocks of code in the SCRIPT file allow the user to reproduce the figures of the 'IIWI paper'.

4.2.1 The f.plot.univar function

This function combines all or a fraction of individual mamo runs corresponding to a simulation study into a single plot representing the density (number of pairs at the end of the simulation per hectare; based on the output mamo variable np, the patch-average elevation-specific number of pairs at the end of the simulation) as a function of the input mamo variable grad (patches elevation).

As usual, the argument output.dir tells the function where the data can be found. The next two arguments, var.excl and val.excl, allow the user to exclude the fraction val.excl of the data corresponding to var.excl. An example will be given later. Next, we present arguments concerning the plot characteristics. The argument ylab is the label for the y-axis; col.obs allows the user to choose the color for the non-simulated (observed) data y.obs, plotted together with the simulations if the argument add.y.obs = TRUE; margin.up allows the user to modify the range of the y-axis; several attempts may be needed to find the optimal value of margin.up that does not leave data outside the plot, or create an empty space at the top. Ideally, modifying the range of the y-axis should be entirely automatic but the current version of MAMO is manual for technical reasons that will not be discussed here. So please be warned: make at least one attempt where margin.up is big (say > 2) to make sure you know where your data stop before picking a (smaller, including possibly negative) value of margin.up that produces a clear figure. The argument main concerns the title of the plot, but there is a catch: if main = NA, no title will be added to the plot; otherwise, the title will start with main but will also contain the values chosen for the fixed parameters of the plot. As its name implies, f.plot.univar only allows the user to explore the variation of a single variable. This variable is selected by the argument wch.plot; col.cat allows the user to select a specific color for each category of the selected variable; e.g., if wch.plot = "RISK", five categories (from 1 to 5) have been simulated (we used n.RISK = 5 in our simulation study); the colors in col.cat will be assigned in that same order,
i.e. col.cat[1] is the color that will represent RISK = 1, etc. In addition, if wch.plot = "RISK", then the user has to select val.RISK = NA, while all other variables have to be fixed to a certain value; for instance, val.AC = 3, val.RAT = 1, val.RES.1 = 1, val.RES.2 = 1, which implies we take the simulation set with no evolution of malaria tolerance (remember, we used evol.AC = c(3,2,1) in our simulation study; val.AC = 3 therefore corresponds to evol.AC = 1, i.e. present value of malaria survival is not augmented/multiplied by 1); we also take the simulation set with no increase of resources during the second part of the non-breeding season (val.RES.2 = 1 corresponds to mg.K.NB.2[[1]] in the simulation study, i.e. rep(1, 10)); because we did not explore management scenarios such as reduction of rat predation or increasing resources during the first part of the non-breeding seasons, the only value possible for the arguments val.RAT and val.RES.1 is 1 (n.RAT = 1 and n.K.NB.1 = 1 in our simulation study). Finally, the last set of f.plot.univar arguments concerns the legend which will be added to the Figure at coordinates leg.x and leg.y, with the text, R symbols, line type and colors defined by leg.txt, leg.pch, leg.lty and leg.col, respectively. Note that the legend must include information for observed data if add.y.obs = TRUE (default).

The figure is produced automatically when running f.plot.univar. Individual squares are simulated data points, thin lines are sigmoid clines fitted for individual simulation run, and broad lines are sigmoid clines fitted for average population size at each elevation. As we mentioned in the chapter 2.1.8, the algorithm we are using (nls R function) may fail to estimate the parameters of the cline, for instance if density pattern is not sigmoidal, but also unpredictably when the pattern seems compatible with a sigmoid. To avoid an error which would prevent the figure from being produced, we used the warnonly = TRUE option of nls, which will return a warning message in case of convergence failure. This way, even if convergence has not been reached, nls will provide estimates for the cline parameters. In the case of f.plot.univar, an 'imperfect' cline is added to the plot, but a warning message will be produced. More flexible algorithms, such as generalized additive models, could be implemented in future MAMO versions to replace nls.

The function f.plot.univar also returns two output elements. First, d.subset is the subset of the data resulting from the combination of t.sim.txt and factors.txt that helped produce the Figure. Second, f.plot.univar also returns test.mamo which is the maximum value of the mamo output test.disp.breed generated during the simulation study; test.mamo should have a value close to zero (typically ~ 10^-5); if it is larger than ~ 10^-3, it may be advisable to re-run the simulation study using calc.gamma.d = "slow.robust", though this will take much longer.

Below, we include the code from BLOCK 6 of the SCRIPT file as an example of f.plot.univar, yielding Fig. 4.2.1-1, which is identical to Fig. 5 of the 'IIWI paper'.

```r
# BLOCK 6
# Fig. 5 of the 'IIWI paper'
f.plot.univar( output.dir = "C:/Programs/MAMO/RUN/IIWI.1_1", var.excl = NA, val.excl = NA, ylab = "# pairs IIWI / ha of native forest", main = NA, col.obs = "red", margin.up = 0, y.obs = y.obs.IIWI.1, wch.plot = "RISK", col.cat = c("grey90", "grey70", "pink", "grey40", "black"), val.RISK = NA, val.AC = 3, val.RAT = 1, val.RES.1 = 1, val.RES.2 = 1,
```
Below is another example of using the function `f.plot.univar`. We reproduce Fig. 4.2.1-1 using only the fraction of the simulation study that corresponds to present and future climatic conditions without management (i.e. factors.txt RISK=3 or 5). In addition, we change the argument `main` from NA to "IIWI" creating a title starting with 'IIWI', followed by our choice of parameter values for other 'fixed' parameters (Fig. 4.2.1-2). Here is the corresponding code, as modified from BLOCK 6:

```r
f.plot.univar(output.dir = "C:/Programs/MAMO/RUN/IIWI.1_1", var.excl = rep("RISK", 3), val.excl = c(1, 2, 4), ylab = "# pairs IIWI / ha of native forest", main = "IIWI", col.obs = "red", margin.up = 0, y.obs = y.obs.IIWI.1, add.y.obs = TRUE, wch.plot = "RISK", col.cat = c("pink", "black"), val.RISK = NA, val.AC = 3, val.RAT = 1, val.RES.1 = 1, val.RES.2 = 1, leg.x = 1, leg.y = 4.5, leg.text = c("Past", "Pres / 2", "Pres-obs", "Pres-sim", "2100/2", "2100"), leg.pch = c(15, 15, 3, 15, 15), leg.lty = c(2, 2, 1, 2, 2), leg.col = c("grey90", "grey70", "red", "pink", "grey40", "black")
)
```

4.2.2 The `f.plot.bivar` function

Like `f.plot.univar`, this function combines all or a fraction of individual `mamo` run from the simulation study into a single plot. Unlike `f.plot.univar`, however, `f.plot.bivar` is not limited to plotting the output `mamo` variable `np` (patch-average elevation-specific number of pairs at the end of the simulation) as a function of the input `mamo` variable `grad` (patches elevation). Instead, it can plot any quantitative or semi-quantitative variable, `y` (the argument for the response variable on the y-axis), as a function of two explanatory factors, namely `x` (the argument for the explanatory variable on the x-axis) and the offset factor `o`. Note that for plotting purpose `f.plot.bivar` is essentially a wrapper of the function `raw.means.plot` of the R package `plotrix`. Accordingly, it plots both raw data in the background (open symbols) and factor means in the foreground (filled symbols) to provide a more accurate visualization of the underlying distribution.
Fig. 4.2.1-1. 'I'iwi distribution along the elevational gradient. Predicted 'I'iwi density (# pairs ha⁻¹) is plotted for pre-malaria (light grey), present (pink), current malaria transmission risk / 2 (medium grey), and future climatic conditions (dark grey = malaria transmission risk in 2100 / 2, black = 2100). Individual squares are simulated data points, thin dashed lines are sigmoid clines fitted for individual simulation run, and broad dashed lines are sigmoid clines fitted for average density during the corresponding period. The observed current 'I'iwi population size is shown by red crosses and the solid red sigmoid curve. Only simulations corresponding to the current level of malaria mortality (AC = 3, i.e. Sm.ac = 0.13) and resources during the second period of the non-breeding season (RES = 1, i.e. no supplementation) are included.

Some f.plot.bivar arguments are identical to the ones used in f.plot.univar, including output.dir (location of the data), var.excl (variable(s) to exclude) and its companion val.excl (value(s) of the variable(s) to exclude). The arguments val.RISK, val.AC, val.RAT, val.RES.1 and val.RES.2 also have the same function; but this time since there are two explanatory factors, identified by the arguments x and o, the two 'value' arguments corresponding to x and o must be set to NA (e.g., if x = "AC" and o = "RISK", then val.AC = NA and val.RISK = NA). Unlike f.plot.univar, f.plot.bivar has an argument called take.subset (logical). If take.subset = TRUE (default) and the remaining 'value' arguments (in our example, val.RAT, val.RES.1 and val.RES.2) are not set to NA, then a subset of the data containing only the chosen values will be kept and plotted (e.g., val.RAT = 1, val.RES.1 = 1 and val.RES.2 = 1, corresponding to no management action against rats and no increase of nectar resources). The argument main also has the same function as it does in f.plot.univar, i.e. no title will be printed when set to NA, otherwise a title indicating the values taken by the three factors different than x or o. Note that if take.subset = FALSE and main is not set to NA, the 3 non-explanatory factors will have to be set manually to NA, otherwise the title (but not the plot) may be misleading. Finally, be aware that in the current version of MAMO (as mentioned earlier; see chapter 4.1 concerning the f.run function), there is no 'RAT' column/factor in the simulation study output; instead, two columns named RAT.S and RAT.F are produced. Therefore, the user has to choose either one of them as the x
or o factor (e.g, x = "RAT.S") in order to visualize the effect of rat management (currently, RAT.S and RAT.F are always identical as we assume that rat management does not affect differently adult and fledging survival). Future versions of MAMO could achieve a simpler and more coherent design, for instance by merging the columns RAT.S and RAT.F into a single 'RAT' column within 'factors.txt'.

The remaining f.plot.bivar arguments are ylab and xlab, the labels on the y- and x-axis, respectively; title.o is the title given to the legend on the right of the figure concerning the offset explanatory factor if the argument legend.o = TRUE (default); l.pos is a numeric vector of length 2 indicating the position of the legend; if not specified, it is automatically determined.

The outputs of f.plot.bivar are:
1) the plot, produced automatically;
2) d.subset, the subset of the data, from the combination of t.sim.txt and factors.txt, used to produce the figure;
3) test.mamo which is the maximum value of the mamo output test.disp.breed generated during the simulation study; test.mamo should have a value close to zero (typically ~ 10^{-5}); if it is larger than say ~ 10^{-3}, it may be advisable to re-run the simulation study using calc.gamma.d = "slow.robust" (will take much longer!); 4) a print on the console of the results of two mixed-effect linear models testing the influence of the explanatory factors x and o on the response factor y while accounting for the rank in the 'demographic envelop' and replicate number of each unique parameter combination (columns 'ENVP' and 'SIM' of factors.txt, respectively, treated as random factors - intercepts only-):
   i) full model including interaction between x and o;
   ii) additive model between x and o (no interaction)

One example of using f.plot.bivar is illustrated with the part of BLOCK 7 that creates Fig. 6 of the 'IIWI paper' (Fig. 4.2.1-1). The rest of the BLOCK 7 code, which allows the user to extract some of the statistics used in the paper, such as the fraction of IIWI remaining in comparison to the pre-malaria era, will not be discussed here as it does not relate to f.plot.bivar.

```r
# BLOCK 7
# Fig. 6 of the 'IIWI paper'
z = f.plot.bivar(  
output.dir = "C:/Programs/MAMO/RUN/IIWI.1_1",  
```
var.excl = NA, val.excl = NA,
take.subset = TRUE, val.RISK = NA, val.AC = NA, val.RAT = 1, val.RES.1 = 1, val.RES.2 = 1,
y = "np.metapop", ylab = "# pairs IIWI in metapopulation", main = NA,
x = "AC", xlab = "Malaria mortality",
o = "RISK", title.o = "RISK", legend.o = TRUE, l.pos = NA

# add observed data point
np.metapop.obs = sum(y.obs.IIWI.1* 100)  * 2

# we multiply by 100 y.obs.IIWI.1 to get # pairs / Km2 at each elevation (from # pairs / ha)
# because unit = 1 and 1 Km2 covers ~ 100 m in elevation (see IIWI paper), sum gives the
#total number of pairs along the gradient ( 1 single column)
# because nc = 2, we multiply by 2 to obtain the observed metapopulation abundance
points(3, np.metapop.obs, col = "red", pch = 3, cex = 1.8, lwd = 2)

# differentiate the different categories of the parameter gamma.mov in the future
k = 0.2
di = z$d.subset
di = di[di$AC == 3 & di$RISK == 5,]
di.m1 = di[di$gamma.mov == 0.159,]; di.m2 = di[di$gamma.mov == 0.541,]; di.m3 =
di[di$gamma.mov == 10,]
points(di.m1$AC+k, pch = 25, cex = 1.8, di.m1$np.metapop, col = "blue", lwd = 2)
points(di.m2$AC+k, pch = 25, cex = 1.8, di.m2$np.metapop, col = "purple", lwd = 2)
points(di.m3$AC+k, pch = 25, cex = 1.8, di.m3$np.metapop, col = "red", lwd = 2)

Another example of using f.plot.bivar is illustrated below using the part of BLOCK 8 that creates
Fig. 7 of the 'IIWI paper' (Fig. 4.2.2-2). The rest of the BLOCK 8 code, which allows the user to
extract statistics such as the fraction of IIWI remaining as compared to the pre-malaria era, will
not be discussed here as it does not relate to f.plot.bivar.

# BLOCK 8
# Fig. 7 of the 'IIWI paper'
layout(matrix(c(1:3), 3, 1)); par(mar = c(3.6,3.6,0,0)+0.5, cex.main = 1)

i = f.plot.bivar(
output.dir = "C:/Programs/MAMO/RUN/IIWI.1_1",
var.excl = NA, val.excl = NA,
take.subset = TRUE, val.RISK = NA, val.AC = NA, val.RAT = 1, val.RES.1 = 1, val.RES.2 = 1,
y = "np.high", ylab = "# pairs IIWI - 1800m", main = NA,
x = "AC", xlab = ",
o = "RISK", title.o = "RISK", legend.o = TRUE, l.pos = NA
)

# add observed data point
np.1800.obs = y.obs.IIWI.1[2] * 100
points(3, np.1800.obs, col = "red", pch = 3, cex = 1.8, lwd = 2)
# differentiate the different categories of the parameter gamma.mov in the future
k = 0.2
di = i$d.subset
di = di[di$AC == 3 & di$RISK == 5,]
di.m1 = di[di$gamma.mov == 0.159,]; di.m2 = di[di$gamma.mov == 0.541,]; di.m3 = di[di$gamma.mov == 10,]
points(di.m1$AC+k, pch = 25, cex = 1.8, di.m1$np.high, col = "blue", lwd = 2)
points(di.m2$AC+k, pch = 25, cex = 1.8, di.m2$np.high, col = "purple", lwd = 2)
points(di.m3$AC+k, pch = 25, cex = 1.8, di.m3$np.high, col = "red", lwd = 2)

#---
j = f.plot.bivar(output.dir = "C:/Programs/MAMO/RUN/IIWI.1_1",
var.excl = NA, val.excl = NA,
take.subset = TRUE, val.RISK = NA, val.AC = NA, val.RAT = 1, val.RES.1 = 1, val.RES.2 = 1,
y = "np.mid", ylab = "# pairs IIWI - 1500 m", main = NA,
x = "AC", xlab = "",
o = "RISK", title.o = "RISK", legend.o = TRUE, l.pos = NA)

# add observed data point
np.1500.obs = y.obs.IIWI.1[5] * 100
points(3, np.1500.obs, col = "red", pch = 3, cex = 1.8, lwd = 2)

#---
k = f.plot.bivar(output.dir = "C:/Programs/MAMO/RUN/IIWI.1_1",
var.excl = NA, val.excl = NA,
take.subset = TRUE, val.RISK = NA, val.AC = NA, val.RAT = 1, val.RES.1 = 1, val.RES.2 = 1,
y = "np.low", ylab = "# pairs IIWI - 1200 m", main = NA,
x = "AC", xlab = "Malaria mortality",
o = "RISK", title.o = "RISK", legend.o = TRUE)

# add observed data point
np.1200.obs = y.obs.IIWI.1[8] * 100
points(3, np.1200.obs, col = "red", pch = 3, cex = 1.8, lwd = 2)
Fig. 4.2.2-1. Total number of pairs of 'iwi in the metapopulation as a function of mortality and transmission risk of malaria. The study area comprises a total of 20 square patches (1 km$^2$ each) spread across ten 100-meter elevational bands (2 patches per elevation). Patch centers range from 1,000 to 1,900 m. The x-axis represents the probability that an individual will die from malaria infection (malaria mortality): 1 = 0.61, 2 = 0.74, 3 = 0.87 (current estimate). The malaria transmission risk is evaluated: 1 = Pre-malaria (transmission risk null); 2 = current risk / 2; 3 = present risk; 4 = risk in 2100 / 2; and 5 = risk in 2100. The observed current 'iwi population size is shown by a red cross. Simulations are shown in open black symbols (filled symbols = simulation averages, connected by lines), except for malaria mortality = 3 and risk = 5: blue corresponds to $\gamma_{\text{mov}} = 0.159$ (small propensity to migratory movements), purple to $\gamma_{\text{mov}} = 0.541$, and red to $\gamma_{\text{mov}} = 10$ (no resistance to migratory movements). Only simulations corresponding to the current level of resources during the second period of the non-breeding season (RES = 1) are included.
4.2.3 The f.plot.composite function

This function is related to (and modified from) f.plot.univar; like this function, f.plot.composite aims at combining all or a fraction of individual mamo runs corresponding to a simulation study into a single plot representing the density (number of pairs per hectare at the end of the simulation) as a function of elevation. Two main differences are:

1) unlike f.plot.univar, f.plot.composite only plots the sigmoid clines fitted for average population size at each elevation; simulated data points and sigmoid clines fitted for individual simulation run are not shown. Letting go of the variability and uncertainty allows the user to focus on the expected effect size of a given management action;

2) f.plot.composite has a new argument called create.plot (logical). If create.plot = TRUE, the figure is created from scratch; but if create.plot = FALSE, only the clines are added to a pre-existing plot. Hence, while f.plot.univar only allows the user to explore the variation of a single variable, it is possible to explore two or more variables by repeatedly calling f.plot.composite, the first time with the argument create.plot = TRUE, and thereafter with the argument create.plot = FALSE (see example below).

Most of the remaining arguments are identical between f.plot.univar and f.plot.composite, including output.dir, var.excl, val.excl, ylab, main, margin.up, val.RISK, val.AC, val.RAT, val.RES.1, val.RES.2, leg.x, leg.y, leg.text, leg.pch, leg.lty, and leg.col.

Because f.plot.composite focuses on comparative simulation results, it does not plot the observed data, and the following arguments are discarded: add.y.obs, col.obs, y.obs.

Finally, four more arguments are specific to f.plot.composite:

1) if fig.title is not set to NA, then the figure title is fig.title; otherwise, it will be defined by main (see main description in f.plot.univar for specifics); hence, fig.title can override main;
2) *add.cline.cat* is a vector telling *f.plot.composite* whether it should fit a cline for a specific value of the argument *wch.plot*; for instance, let's assume *wch.plot = "RISK"* with five categories (1 to 5); if *add.cline.cat = c("FALSE", rep("TRUE", 4))*, we tell *f.plot.composite* to fit a cline when *RISK > 1*, but not when *RISK = 1*; it may make sense because in the latter case we simulated pre-malaria condition; assuming a spatially constant carrying capacity, no spatial cline is to be expected. Hence, when *add.cline.cat = FALSE*, instead of a cline *f.plot.composite* adds an horizontal line corresponding to the mean value of the response variable;

3) *add.leg* allows the user to decide whether the legend should be added to the plot;

4) *lty.mean* is the line type to be used for the clines (same value as the R *lty* parameter: 1 = solid, 2 = dashed, 3 = dotted, etc.).

As an example, we may want to explore the consequence of increasing nectar resources during the second part of the non-breeding season (coded by *wch.plot = "RES.2"* and *val.RES.2 = NA*), but not only at a given, fixed time period (as would be the case with *f.plot.univar*), but comparatively at different levels of malaria transmission risk:

i) in the present (without management): *val.RISK = 3*; first calling of *f.plot.composite*

ii) in 2100 but after reducing the risk of malaria transmission risk by 50%, so-called '2100/2': 
*val.RISK = 4*; second calling of *f.plot.composite*

iii) in 2100 but without management: *val.RISK = 5*; third calling of *f.plot.composite*

The code producing this Figure (Fig. 4.2.3-1 = Fig. 8 of the 'IIWI paper') is given in BLOCK 9 of the SCRIPT file and reproduced below. Since *wch.plot = "RES.2"*, each time *f.plot.composite* is called, 3 different levels of resource management are plotted: no increase of nectar (control), a 50% increase at high elevations (1700 to 1900 m), and a 100% increase at the same high elevations.

# BLOCK 9
# Fig. 8 of the 'IIWI paper'

```r
def.plot.composite(output.dir = "C:/Programs/MAMO/RUN/IIWI.1_1",
ylab = "# pairs IIWI / ha of native forest", fig.title = NA, main = NA, margin.up = -0.5,
wch.plot = "RES.2", col.cat = c("black", "grey70", "grey90"), add.cline.cat = rep("TRUE", 3),
val.RISK = 3, val.AC = 3, val.RAT = 1, val.RES.1 = 1, val.RES.2 = NA,
add.leg = TRUE,
leg.x = 1, leg.y = 5,
leg.text = c("Present", "Present (RES×1.5 | high)", "Present (RES×2 | high)", "2100/2", "2100/2 (RES×1.5 | high)", "2100/2 (RES×2 | high)", "2100", "2100 (RES×1.5 | high)", "2100 (RES×2 | high)"),
leg.pch = NA, leg.lty = c(rep(1,3), rep(2,3), rep(3,3)), leg.col = c(rep(c("black", "grey70", "grey90")), 3)),
create.plot = TRUE, lty.mean = 1)
```
output.dir =
"C:/Programs/MAMO/RUN/IIWI.1_1",
ylab = "# pairs IIWI / ha of native forest",
fig.title = NA, main = NA, margin.up = -0.5,
wch.plot = "RES.2", col.cat = c("black",
"grey70", "grey90"), add.cline.cat =
rep("TRUE", 3),
val.RISK = 4, val.AC = 3, val.RAT = 1,
val.RES.1 = 1, val.RES.2 = NA,
add.leg = FALSE,
create.plot = FALSE, lty.mean = 2
)
f.plot.composite(
output.dir =
"C:/Programs/MAMO/RUN/IIWI.1_1",
ylab = "# pairs IIWI / ha of native forest",
fig.title = NA, main = NA, margin.up = -0.5,
wch.plot = "RES.2", col.cat = c("black",
"grey70", "grey90"), add.cline.cat =
rep("TRUE", 3),
val.RISK = 5, val.AC = 3, val.RAT = 1,
val.RES.1 = 1, val.RES.2 = NA,
add.leg = FALSE,
create.plot = FALSE, lty.mean = 3
)
abline(v = 1.7, lty = 4)

Fig. 4.2.3-1. Effect of our virtual management experiment - increasing nectar resources at high elevations (1,700 to 1,900 m) during the second period of the non-breeding season (nb.2). Predicted ‘I’iwi density (# pairs ha⁻¹) is plotted for present, future (2100), and transitory (called ‘2100/2’) climatic conditions as a function of the level of resources at high elevations: black = no change as compared to present, medium grey = 1.5 times more bloon at high elevations than present, light grey = 2 times more bloon at high elevations than present. Lines are sigmoid clines fitted for the corresponding treatment, after averaging individual simulation run to obtain a single average population size at each elevation. Only simulations corresponding to the current level of malaria mortality (AC = 3, i.e. Sm.ac = 0.13) are included.
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LITERATURE CITED


APPENDIX I: THE IIWI PAPER

Altitudinal migration and the future of an iconic Hawaiian honeycreeper in response to climate change and management

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Abstract. Altitudinal movement by tropical birds to track seasonally variable resources can move them from protected areas to areas of increased vulnerability. In Hawai‘i, historical reports suggest that many Hawaiian honeycreepers such as the ‘i‘iwi (Drepanis coccinea) once undertook seasonal migrations, but the existence of such movements today is unclear. Because Hawaiian honeycreepers are highly susceptible to avian malaria, currently minimal in high-elevation forests, understanding the degree to which honeycreepers visit lower elevation forests may be critical to predict the current impact of malaria on population dynamics and how susceptible bird populations may respond to climate change and mitigation scenarios. Using radio telemetry data, we demonstrate for the first time that a large fraction of breeding adult and juvenile ‘i‘iwi originating from an upper-elevation (1,920 m) population at Hakalau Forest NWR exhibit post-breeding movements well below the upper elevational limit for mosquitoes. Bloom data suggest seasonal variation in floral resources is the primary driver of seasonal movement for ‘i‘iwi. To understand the demographic implications of such movement, we developed a spatial individual-based model calibrated using previously published and original data. ‘I‘iwi dynamics were simulated backwards in time, to estimate population levels in the absence of avian malaria, and forwards in time, to assess the impact of climate warming as well as two potential mitigation actions. Even in disease-free ‘refuge’ populations, we found that breeding densities failed to reach the estimated carrying capacity, suggesting the existence of a seasonal 'migration load' as a result of travel to disease-prevalent areas. We predict that ‘i‘iwi may be on the verge of extinction in 2100, with the total number of pairs reaching only ~ 0.2 to 12.3% of the estimated pre-malaria density, based on an optimistic climate change scenario. The probability of extinction of ‘i‘iwi populations, as measured by population estimates for 2100, is strongly related to their estimated migration propensity. Long-term conservation strategies likely will require a multi-pronged response including a reduction of malaria threats, habitat restoration and continued landscape-level access to seasonally variable nectar resources.

Key words: altitudinal migration; avian malaria; climate change; conservation; demographics; ‘i‘iwi; individual-based model; Hawai‘i; telemetry.
Introduction

Animal migration, typically considered as an adaption to increase fitness in a spatially and seasonally variable environment, can present great challenges to the conservation of species. First, seasonal migrants can face different threats on their breeding, non-breeding, and migratory grounds. For many tropical bird species, even those considered non-migratory, non-breeding habitat may differ from breeding habitat as individuals track seasonally variable resources or attempt to escape severe storms, particularly across elevations (Chaves-Campos et al. 2003, Boyle et al. 2010). Such seasonal movements can take individuals away from safe areas (such as reserves) into areas with increased risk of mortality due to fragmentation, predators, and disease (Chaves-Campos et al. 2003). Furthermore, carryover effects can have profound implications on population dynamics with effects from one season potentially influencing condition, breeding success and survival in subsequent seasons (e.g., Alves et al. 2013). Finally, anthropogenic climate change has become a significant new source of concern (Thomas et al. 2011, Foden et al. 2013), notably by changing the distribution of threats in unexpected ways.

Landscapes that are highly heterogeneous or have strong gradients of resources or threats should present the greatest challenges to mobile animals. Areas of high contrasts are common in the tropics, such as along elevational gradients, and one of the most well-known examples is in Hawai‘i. Hawaiian tropical forests are highly fragmented, and deforestation and introduced plants, animals, and diseases have created a complex environment for the native forest birds. Hawai‘i’s forest birds, many of which are foraging specialists, are characterized by a high percentage of threatened endemic forms constituting the single most important ecoregion for the conservation of forest-dependent birds in the world (Buchanan et al. 2011).

Today most species of Hawaiian native forest birds are restricted to isolated high elevation forests (e.g., Scott et al. 1986). Causes for the current distribution include habitat loss (near complete loss of native forest in low elevations, logging and overgrazing by introduced ungulates in the mountains), introduced plants, predators, avian competitors, and mosquito-borne disease. In particular, avian malaria (*Plasmodium relictum*) is believed to play a major role in limiting the distribution and population size of many native forest birds, particularly Hawaiian honeycreepers such as ‘i‘iwi (*Drepanis coccinea*) which are highly susceptible to disease (Van Riper et al. 1986, Atkinson et al. 1995, Samuel et al. 2011, Samuel et al. 2015). The only identified mosquito vector for malaria (*Culex quinquefasciatus*) has an upper elevational limit of approximately 1,475 m for self-sustaining populations, and 1,715 m for warm season migrating populations based on minimal thermal requirements for development
(Ahumada et al. 2004). With few exceptions, populations of native forest birds are restricted to high-elevation refugia climatically unsuitable for pathogen and mosquito development (LaPointe et al. 2010, Samuel et al. 2011). However, food tracking and storm-driven movement can bring them to lower elevation areas with active disease transmission, and global warming threatens to move disease into upper elevation forests (Benning et al. 2002, Hart et al. 2011, Samuel et al. 2011, Liao et al. 2015).

In Hawai'i, early naturalists described large seasonal 'migration' of birds, particularly nectarivores such as 'i'iwi and 'apapane (*Himatione sanguinea*), presumed to track flowering resources both within and across the elevational gradients (Warner 1968). In addition, prolonged winter storms or hurricanes would often result in highland birds being driven into lowland valleys (Perkins 1903). Such altitudinal shifts, which were prominent during the early historical period when the native bird populations were more or less intact, were presumably adaptive by increasing available resources and providing safety from extreme climatic events. However, these historical altitudinal migrations may be collapsing in the face of habitat loss and disease, with recent studies suggesting marked reductions in seasonal movements of 'i'iwi and 'apapane (Ralph & Fancy 1995, Hess et al. 2001, Hart et al. 2011). The apparent reduction or disappearance of seasonal movements of these nectarivores could be from far fewer birds present today than in the past (due to continuing population declines) making movement patterns more difficult to detect. Alternatively, competition for nectar resources may not be as intense as it once was due to reduced populations of extant species and the extinction of dominant nectarivore competitors (such as the Hawai'i 'ōō [*Moho nobilis*] and the Hawai'i Mamo [*Drepanis pacifica*]), which frequently chased smaller honeycreepers from flowering trees (Banko & Banko 2009). Additionally, populations may be evolving to have more sedentary individuals given the high selective pressure likely on individuals with a propensity to follow flowering peaks into malaria-infested areas (Hart et al. 2011).

In this paper, we used the disease-susceptible 'i'iwi as a model species to understand how seasonal movement patterns, along with the current and future distribution of disease across the landscape, can interact to impact long-term population dynamics. The 'i'iwi, a bright red bird with large decurved bill, is one of the most spectacular member of the endemic Drepanidini tribe of Hawaiian honeycreepers. It breeds and winters primarily in mesic and wet forests dominated by 'oh'a (*Metrosideros polymorpha*) and koa (*Acacia koa*) trees (Fancy & Ralph 1998), and may once have been the most widespread of the Hawaiian honeycreepers, found on all the major islands from sea level to tree line. Although the 'i'iwi is still relatively abundant in high elevation forests of Hawaii and east Maui islands, the species has been extirpated from over 90% of its historical range and is being considered for listing under the
Endangered Species Act (Paxton et al. 2013). Two factors suggest it is likely to be very sensitive to the effects of the forthcoming climate warming. First, the ‘i’iwi is highly susceptible to avian malaria with the highest rate of malaria mortality among the Hawaiian honeycreepers tested so far (Atkinson et al. 1995, Samuel et al. 2015). As a result, ‘i’iwi is now essentially restricted to high-elevation disease-free forests. However, because mosquito and malaria dynamics are strongly controlled by temperature and rainfall, future climate warming will likely have negative impacts on native bird populations even in high elevation forests (Fortini et al. 2015, Liao et al. 2015). Second, the ‘i’iwi is recognized as a highly mobile species, with individuals frequently observed flying high above the canopy (Perkins 1903, Ralph & Fancy 1995). Seasonal movement up and down montane habitats is widely thought to be related to post-breeding tracking of flowering ‘ohi’a, the dominant canopy tree species (MacMillen and Carpenter 1980, Scott et al. 1986, Ralph & Fancy 1995, Berlin et al. 2001, Hart et al. 2011). Given ‘i’iwi’s susceptibility to avian malaria, determining their use of lower elevations where malaria transmission is higher and will likely increase in the future may be critical to accurately predict their current dynamics and their response to climate change and mitigation scenarios. In addition, non-breeding season movements of ‘i’iwi could reduce the effectiveness of reserves that only protect high-elevation forests, as significant mortality outside the reserve during the non-breeding season could affect the core breeding population.

We used radio telemetry to document for the first time long-distance movements during the non-breeding season in a high elevation breeding population of ‘i’iwi on Hawai‘i Island. The long-distance tracking of individuals allowed us to assess whether such movement exposed birds to higher malaria infection risk at lower elevations, to determine whether individuals left a reserve area managed for forest bird preservation and to identify important non-breeding habitat. In parallel, we measured patterns of ‘ohi’a flowering along an elevational gradient to understand how movement patterns may relate to resource distributions. Next, we developed a spatial model aimed at better understanding how movement and the distribution of avian malaria risk interact to affect population dynamics and species viability in a context of changing climate and increasing disease risk. We parameterized and calibrated the model using a wide array of previously published and original data, including seasonal movement, seasonal patterns in bloom, and projections of current and future malaria intensity and distribution. We simulated ‘i’iwi dynamics both backwards in time, to estimate population levels in the absence of avian malaria, and forwards in time, to assess the impact of climate warming as well as two potential mitigation actions.
Materials and Methods

Study site
'I'iwi were studied at Hakalau Forest National Wildlife Refuge (hereafter, Hakalau) on the windward eastern slope of Mauna Kea (Hamakua region), Hawai‘i Island, which has the highest 'i'iwi density across the species’ range (Paxton et al. 2013). The Hamakua region is covered by a largely contiguous wet-mesic and montane forest from approximately 2,000 m (current treeline) to 600 m above sea level, composed largely of ‘ohi’a and koa trees, below which forest has been converted to agriculture or else is heavily degraded by non-native vegetation. The native forest is managed by multiple entities including US Fish and Wildlife Service, the State of Hawai‘i (Laupahoehoe Natural Area Reserve, Laupahoehoe and Hilo Forest Reserves, and Department of Hawaiian Homelands), and private landowners, but currently only Hakalau is managed primarily for forest bird habitat.

Seasonal movements
In 2003 and 2004, at the end of the breeding season (March–June), ‘i‘iwi from a high elevation study site of Hakalau (Pua ‘Akala, 1920 m: Fig. 1) were fitted with VHF pulse radio-transmitters. Transmitters had a 3–6 week battery life, weighed less than 5% of a bird’s body weight, and were attached to birds using a figure-eight harness with elastic cording (Rappole & Tipton 1991). The majority of individuals were known breeders and/or offspring from the study site based on a multi-year banding and nesting study (Kuntz 2008). Male and female ‘i‘iwi are monochromatic and were sexed in the hand using reproductive characters or morphometrics (Fancy & Ralph 1998).

Birds were tracked using both ground and aerial telemetry. However, due to the rugged, roadless terrain across most of the Hamakua region, the majority of individuals tracked outside of the Pua ‘Akala study site were located during 2–3 hour survey flights over the eastern Mauna Kea forest from May–August in 2003 and 2004. Aerial surveys were conducted from a fixed wing monoplane with directional Yagi antenna attached to each strut approximately every 10 days depending on weather and pilot availability (12 flights each in 2003 and 2004). The plane flew ~2 km transects over the forest in attempt to locate all active transmitters, with an average of 67% of possibly active transmitters located per flight. When a transmitter signal was heard, time, signal directional and location (UTM) of plane was recorded from multiple locations to allow for subsequent triangulation to estimate bird location. Plane locations and bearings were brought into a GIS environment (ARCVIEW, version 3.2; ESRI, Redlands, California) for triangulation, with an estimated error (based on known points) of ± 1,000 meters. Aerial signals could be located up to 3 km away, although distances
varied depending on battery strength and bird orientation. Monthly, ground surveys were conducted using an omni antenna attached to a vehicle along an upper elevation road above the forest, along refuge roads (Maulua and Nauhi tracts from 1,580 m to 2,000 m elevation) and on a single track in Laupahoehoe Natural Area Reserve (NAR) (985 m to 1,475 m: Fig. 1). Signal ground transmission in the mid elevation forest was limited to approximately 500–1,000 m. Once a ground signal was heard, a Yagi directional antenna was used to triangulate a location. Because the objective of the telemetry study was to detect long-distance movement rather than migration propensity and roosting locations (model parameter \( \gamma_{\text{mov}} \)), we present the estimated location of individuals when greater than 1 km from capture location (without integration of error estimate of \( \pm 1,000 \) meters), and estimate parameter \( \gamma_{\text{mov}} \) based on the model calibration procedure (below). Hereafter, distances greater than 1 km from the breeding site are called long-distance locations.

To characterize long-distance movements, we used two response variables, namely distance (from the breeding site) and elevation as well as four explanatory factors, namely sex, age (adult vs. juvenile), season (\( \text{nb.1 vs. nb.2} \), see below) and year (2003 vs. 2004). The relationship between response and explanatory variables was assessed using linear mixed-effect models. To account for the fact that some individuals contributed multiple movements we included a random intercept for each individual. We run four different linear mixed-effect models, two for each response variable (distance and elevation) based on sample size of explanatory factors: the first one was an additive model including age, sex, and season as fixed-effect factors (\( n = 107 \)) while the second one included only sex as fixed-effect factor (\( n = 83 \); in our sample the sex of juveniles was not determined (Kuntz 2008)). All model residuals were normally distributed after accounting for multiple tests using Bonferroni correction (all \( P > 0.0125 \), i.e. 0.05/4).

**Distribution of resources**

Concurrent with radio tracking of 'i'iwi, 'ohi'a flowering (bloom) was recorded along an elevational transect (approximately every 0.8 km along a jeep trail) in Laupahoehoe NAR (Fig. 1). Nine stations were established in 2003 (June–August: 770–1,470 m) and four additional stations were added in 2004 (May–July: 320 m to 1,470 m). We subsequently discarded stations below 950 m because the vast majority (98.1\%) of 'i'iwi telemetry records were above this limit (Fig. 1); in addition, point count surveys at lower elevations along the Laupahoehoe transect failed to detect any 'i'iwi in 2003 and 2004 (not shown). Approximately monthly (depending on weather), the intensity of 'ohi'a flowering was recorded at each station. 'Ohi'a flowers form composite inflorescences or clusters about 5–8 cm wide on the terminal ends of branches, ranging
in color from red to yellow which contrasts with the foliage. The percentage of the crown that was covered in inflorescences was estimated to derive a percent flowering for a single tree (following Scott et al. 1986), and then averaged over the 10 nearest canopy ‘ohi’a to determine the mean ‘ohi’a bloom per station. The same protocol was used at the Pua ‘Akala breeding site, where the mean ‘ohi’a bloom was estimated within about a week of each elevational transect.

The model

Our model is a spatial individual-based (female only) model. The objective is to create a population by simulating fates of individuals. The complete model description, including mathematical details, is given in Appendix S3. A summary of parameter definitions and the parameter values used for simulation are given in Appendix S4. A flow chart summarizing the model is presented in Fig. 2 (lower part). The model was developed as a Decision Support Tool, named ‘MAMO’, based on the name of an extinct Hawaiian honeycreeper and an acronym of ‘Models for Avian Management Optimization’.

Virtual individual birds in simulations, hereafter called e-birds, are grouped into two age classes which breed, survive, and move across a simulated landscape. The simulated landscape is composed of patches that are the sample units for resource and threat levels, as the probabilities associated with these events are patch-dependent. Specifically, the values ascribed to floral resources and malaria transmission risk are elevation-specific and derived from field-based measures (see below). The spatial structure consists of a grid of $i = 1$ to $nr$ rows (modeling elevation) and $j = 1$ to $nc$ columns (which can be simple replicates of elevational patches or model different attributes of the landscape). The spatial structure therefore contains $nr \times nc$ square patches.

Our model is iterative, with the results of one iteration used as the starting point for the next iteration. Each iteration covers one annual cycle (i.e. 365 days). We distinguished three seasonal time-steps within a 1-year iteration, corresponding to the breeding season (September–April) and a non-breeding season that was further subdivided into two periods, non-breeding season 1 ($nb.1$, May–June) and non-breeding season 2 ($nb.2$, July–August), based on telemetry and bloom data (see results). Input parameters such as number of 1-year old and 2+ year old e-birds are used to start the simulation (during year $T = 1$). We used a large number of iterations ($T = 60$ years) for each run to avoid transition effects of the initial conditions and ensure stability was reached for each assessment, namely stable age distribution and population size under corresponding climatic conditions and malaria transmission risk. For instance, to predict the abundance and distribution of ‘i‘iwi in 2100 the climatic conditions and malaria transmission risk corresponding to 2100 were simulated for 60 years, but only the last three (‘at
equilibrium') years of simulation were used to derive summary statistics such as the elevation-specific number of pairs (see below for details).

The breeding population consisted of 1-year old juveniles (produced during the previous breeding season) and adults ≥ 2 years old, as is standard for passerines (Kery and Schaub, 2012). Production of juveniles occurred during the breeding season. Density-dependent regulation was introduced to yield relative stability at carrying capacity. During each season, e-birds may contract malaria and survive or die. Demographic stochasticity in fecundity and survival were modeled using Poisson and Bernoulli processes, respectively (Kery and Schaub 2012). 'Instantaneous' movements between patches may occur three times throughout the annual cycle. Seasonal migration occurs immediately after the breeding season, i.e. at the transition from breeding to nb.1, and also at the transition between nb.1 and nb.2. Natal or breeding dispersal occurs at the end of nb.2 and coincides with the beginning of a new year. After moving, e-birds remained on the patch they selected for the entire duration of the season. The computation of the probabilities associated with each of these events is given in details in Appendix S3, but we summarize below a few elements concerning malaria infection and survival in order to give a better sense of the structure and time unit of the model.

The probability for susceptible e-birds to become infected by malaria was calculated independently for each season (breeding, nb.1 and nb.2) based on the (season-dependent) daily infection rate and the number of days within each season. For instance, if daily rate is $\alpha$ and season lasts $t$ days, the probability to become infected can be simply expressed as $1 - (1 - \alpha)^t$. Importantly, daily rates were also elevation-dependent (see below and Appendix S2). Susceptible e-birds that became infected survived the acute infection with probability $S.m.ac$. Subsequent infection did not incur increased mortality cost (Samuel et al. 2015). Survival probability (independent of malaria) also was calculated independently for each season based on its duration and daily survival rates (different for adults and juveniles: see Appendix S4 for derivation and actual values used after calibration: section S4.2 and Table S2, respectively). For instance, if daily survival rate is $s.d$ and season lasts $t$ days, the probability to survive is $s.d^t$.

We focused our analyses on an elevational gradient ranging from 1,950 to 950 meters above sea level, corresponding approximately to current ‘ohi’a upper forest limit and lower range of non-breeding ‘i‘iwi movements, respectively. The topographical conditions in the Hamakua region are such that the two extremes of the gradient are separated by approximately ten linear kilometers, with fairly constant slope. Accordingly, we built our spatial model as a 10 rows × 2 columns spatial grid containing twenty patches, each covering an area of 1 km$^2$ and an elevational band of 100 m. The
lowest row of two patches goes from 950 to 1,050 meters, and the highest one goes from 1,850 to 1,950 m.

Elevation-specific values were not collected on a 10 × 2 spatial grid that would be the exact physical equivalent of our (virtual) spatial model. The description of how elevation-specific values were obtained is given below. We emphasize that: 1) Our spatial model contains two columns, to allow for elevation-independent movements, but our field sampling was not replicated in a similar fashion; 2) Values along the elevational gradient were not collected every 100 m; instead, we used interpolation and extrapolation techniques to estimate resource and threat values at regular intervals; 3) Resource and threat sampling did not occur in the exact same area, although both occurred on the eastern (windward) side of Hawaii Island: ohī’a flowering was measured in Laupahoehoe NAR (see above and Fig. 1), while malaria transmission risk was based on data collected on the eastern slope of Mauna Loa Volcano (see below; Samuel et al. 2011, Samuel et al. 2015, Liao et al. 2015).

We assumed for simplicity that the carrying capacity during the breeding season ($K.b$), was constant along our elevational gradient (ranging from 950 to 1,950 m), in agreement with the finding that neither ‘ohi’a flower density nor nectar production per inflorescence differed between high-elevation (> 1,650 m) and mid-elevation (1,000–1,300 m) sites on the slopes of Mauna Loa in 2002–2004 (Hart et al. 2011). We used mean ‘ohi’a bloom (see section Distribution of resources) as a proxy for patch quality during the first (May–June) and second period (July–August) of the non-breeding season, as measured by parameters $K.nb.1$ and $K.nb.2$, respectively. Because bloom profiles were very similar in July 2003, August 2003, and July 2004, these data were averaged to estimate a single value for $K.nb.2$. In contrast, we obtained two different estimates for $K.nb.1$, corresponding to the data collected in June 2003 and June 2004, respectively. We performed linear interpolations between available data points to estimate the values for each season all along the gradient (Appendix S1).

We used the malaria-forest bird model developed by Samuel et al. (2011) to estimate daily malaria infection rates (probability of susceptible birds becoming infected with malaria) calibrated for 1,200 and 1,600 m above sea level forests on the eastern (windward) side of Hawaii Island. Current infection rates were based on average temperature and precipitation patterns between 1984 and 2003. Daily malaria infection rates for 2100 were calculated in the same fashion but were based on downscaled temperature and rainfall patterns from an optimistic global climate change scenario (emission scenario RCP4.5, see Liao et al. 2015). We used a two-step approach to estimate the average daily probability of infection ($\alpha$) for each season (breeding = $a.b$, non-breeding 1 and 2 = $a.nb.1$ and $a.nb.2$, respectively) and across
different elevations. First, \( \alpha \) was estimated at 1,200 and 1,600 m by simulating 10^6 susceptible e-birds for the entire season using the estimated (varying) daily infection rates and calculating the proportion of e-birds infected (\( sim.rate \)). For each season of length (\( t \)) the probability of infection can be written as \( 1 - e^{-\lambda_i \cdot t} \), where \( \lambda_i = -\ln(1 - \alpha) \). We therefore inferred \( \alpha = 1 - e^{t \cdot \ln(1 - sim.rate)} \).

Next step was to derive estimates at other elevations. Because the self-sustaining mosquito zone was established at \( \leq 1,475 \) m, and seasonal populations to \( \leq 1,715 \) m (Ahumada et al. 2004), we assumed that the current malaria transmission risk is always zero at elevations higher than 1,715 m. In addition, based on the altitudinal cooling rate (6.4 °C / km) and a predicted temperature increase of 2.3 °C for RCP4.5 in 2100 (Liao et al. 2015), the temperature at 2,000 m in 2100 will be close to what we currently have at 1,600 m. We therefore used the current 1,600 m transmission rate as the future 2,000 m transmission rate in the year 2100. As a first approximation, we performed linear interpolations between available data points, specifically 1,200, 1,600, and 1,800 m for present conditions, and 1,200, 1,600, and 2,000 m for future (2100) projections. A linear extrapolation was used to derive values at elevation < 1,200 m. Because preliminary analyses suggested that quadratic relationships provided a slightly better fit to the actual data (not shown), two quadratic Bézier curves, one convex from 1,200 to 1,600 m, and one concave from 1,200 to 1,000 m, were used for subsequent analyses (note that the difference in terms of risk estimation is small: compare linear and quadratic curves in Appendix S2).

The mosquito that transmits malaria is nocturnal (e.g., Van Riper et al. 1986), and therefore selection of night roosting patches during the non-breeding season is the key component to consider in terms of malaria risk. For simplicity, we assumed that individual e-birds (adults or juveniles) alive at the end of the breeding season selected a single patch for the entire first period of the non-breeding season (\( nb.1 \)) and then selected another patch (potentially identical to the breeding patch or the first non-breeding patch) for the entire second period of the non-breeding season (\( nb.2 \)). Again, the mathematical details underlying the selection of non-breeding patches in the model are given in Appendix S3.

In brief, we assumed that the probability of a given patch (\( n \)) to be selected as the first non-breeding patch of a given e-bird was positively related to the quality of \( n \) (e.g., amount of bloom) during the first period of the non-breeding season, but inversely related to the distance between the e-bird’s breeding patch and \( n \). To account for the effect of distance, we introduced a species-specific migration propensity parameter (\( \gamma.mov \)). When \( \gamma.mov \) is minimal, e-birds always stay in their breeding patch (the effect of distance is overriding; lack of seasonal migration can be due to cost or resistance to movement). For
intermediate $\gamma\cdot mov$ values, e-birds tend to choose non-breeding patches closer to their breeding patch than expected based on resources alone (e.g., partial resistance to movement). Conversely, when $\gamma\cdot mov$ is maximal distance does not impede movement. In this case, the probability for a given patch $n$ to be selected only depends on the proportion of total resources found in $n$ (ideal free distribution). Likewise, the probability of a given patch $n$ to be selected as the second non-breeding patch by a given e-bird was positively related to the quality of patch $n$ during the second period of the non-breeding season, but inversely related to the distance between the e-bird’s first non-breeding patch and $n$. The parameter $\gamma\cdot mov$ was used to control the effect of distance as previously described. Note that there may be a subsequent seasonal movement from the wet forest to the drier subalpine forest at the transition between the non-breeding and breeding seasons (in September-November, which is the period of pair formation: Kuntz 2008), to take advantage of the peak of māmane (*Sophora chrysophylla*) blooming (Hess et al. 2001). Since 'i'iwi are presumed to commute daily and spend the night in wet forests (Scott et al. 1986), while mosquito vectors are active only during the night, these upslope movements are expected to be neutral in terms of malaria transmission risk, and were not accounted for in this model.

At the end of the second period of the non-breeding season, surviving 1-year old juveniles and adults ≥ 2 years old tended to select their natal or former breeding patch, respectively, to start a new breeding season. However, dispersal to a new patch was permitted (details given in Appendix S3). In brief, natal and breeding dispersal distances were calculated using random draws from a log-normal and exponential distribution, respectively. We used a two-step approach to derive the patch-specific transition probability matrix based on natal and breeding dispersal distances, while accounting for patch and grid dimensions and resource distribution during the breeding season. As can be expected, a dispersal event was more likely towards geographically close and high quality patches.

**Summary statistics**

The elevation-specific number of pairs at the end of the simulation is called $np$. This is the average for a single patch. It was obtained by averaging the number of breeding pairs ($n\cdot pairs$) over the last three years of simulation and over the $nc$ columns of the grid, in order to attenuate the effect of demographic stochasticity. The values of $np$ obtained at an elevation of 1,800, 1,500 and 1,200 m are called $np\cdot high$, $np\cdot mid$ and $np\cdot low$, respectively. For illustration purposes, a sigmoid curve was fitted to $np$ values along the elevational gradient $x$ using the formula:
\[a + \frac{b-a}{1 + e^{-K \cdot (x-c)}}\]

where the constants a, b, K and c were obtained using the nls function in R. The total number of pairs in the final population (all patches) was

\[np.\, metapop = nc \times \sum_{k=1}^{nr} np_k.\]

**Model calibration**

The objective of the calibration procedure, detailed in Appendix S4, is to optimize the selection of parameter values of imperfectly known demographic and ecological parameters so that the simulation realistically predicts the response of 'i'iwi to climate change and management (and corresponding to section 'Simulation study'). In that aim, we: 1) Selected a set of 10 imperfectly known demographic and ecological parameters (such as adult survival, fecundity and migration propensity) that were subjected to calibration (see Appendix S4 Table S1 for the full list); 2) Performed a literature review to identify candidate point estimates for these 10 parameters; 3) Performed a pre-simulation model run to select the combinations of candidate point estimates that best predict 'i'iwi's current distribution and abundance along the elevational gradient; 4) Kept a set of 10 best-fitting parameter combinations, the 'demographic and ecological envelope', to test the effects of future climate change and management while explicitly incorporating parameter uncertainty.

In more details, using all candidate values for each of the 10 parameters to calibrate (2-4 each, see Table D2) resulted in 5,184 possible parameter combinations. Without any other information, each of these combinations could be regarded as equiprobable. We therefore used an independent source of data (count data) to determine the combinations that best predicted the current pattern of 'i'iwi distribution along the elevational gradient. Specifically, we: 1) Estimated the current pattern of 'i'iwi distribution along the elevational gradient using the pre-existing Hawai'i Forest Bird Interagency Database (Appendix S4 section S4.1); 2) Selected candidate values for each of 10 parameters based on pre-existing information from the literature (Appendix S4, Table S1 and section S4.2); 3) Candidate parameter values resulted in a total of 5,184 possible combinations; we used MAMO to simulate the resulting elevational distribution of 'i'iwi for each of these combinations; 4) We estimated the fit between the observed and simulated elevational distributions using a least-squares approach, wherein \(fit = -\sum_{i=1}^{nr} (obs_i - sim_i)^2\); with the negative sign, fit is greater (less negative) when the total difference between observed and simulated values - summing across elevations - is small; and 5) We selected the 10 best-fitting runs or parameter combinations (out of 5,184), called the 'demographic and ecological envelope', to run predictive models of 'i'iwi distribution under different threat and management scenarios (Appendix S4, Table S2 and Fig. S1).
**Simulation study**

We simulated population responses of 'i'iwi to different 1) malaria transmission risk (RISK), 2) probability of surviving malaria infection (AC), and 3) resource distribution (RES). Malaria transmission risk was explored with five scenarios. For each scenario, the parameters \( a, b, a_{nb.1} \) and \( a_{nb.2} \) were estimated based on historic conditions (pre-malaria era, i.e. transmission risk null; corresponds to RISK = 1), current climatic conditions (RISK = 3), or on predictions for the year 2100 (RISK = 5; Appendix S2); the fourth and fifth scenarios corresponded to a 50% reduction in present (RISK = 2) or 2100 (RISK = 4) malaria infection risk at every elevation, respectively. This last scenario (RISK = 4) can be regarded as a snapshot of the infection dynamics at approximately 2050, but also as a potential management objective (reducing the transmission risk in 2100 by half), which might be achieved through vector control measures, such as reduction of larval mosquito habitat. Probability of surviving malaria infection was explored with three scenarios characterized by increasing malaria survival rates. The parameter \( Sm.ac \) took values corresponding to the current estimate for 'i'iwi survival (0.13, AC = 3; see Calibration), current estimate \( \times 2 \) (0.26, AC = 2) and current estimate \( \times 3 \) (0.39, AC = 1). This simulation allowed us to investigate the potential benefits of evolutionary change increasing 'i'iwi’s tolerance to malaria, as demonstrated in Hawaiian amakihi (Chlorodrepanis virens; Atkinson et al. 2013; Samuel et al. 2015).

We also explored the consequences of resource distribution using three scenarios where managers increased nectar resources at high elevations during the second part of the non-breeding season (nb.2), when malaria transmission risk is highest (Appendix S2); the first scenario corresponds to no resource supplementation (RES = 1), the second to \( 1.5 \times \) increased resources at elevations \( \geq 1,700 \) m (RES = 2), and the third to \( 2 \times \) increased resources at elevations \( \geq 1,700 \) m (RES = 3).

We accounted for uncertainty in our estimates of demographic and environmental parameters by using the specific parameter combination corresponding to each of the selected 10 best-fitting calibration runs (Fig. 2, Appendix S4 Table S2), with two replicates for each to account for demographic stochasticity. Thus, we had 20 estimates which were averaged to obtain a final estimate. Note that a larger number of replicates would be necessary if stochasticity was expected to play an important role in our analyses, for instance if stochastic extinction was likely. We did not expect it to be the case here for two reasons: 1) we expected the role of demographic stochasticity to be negligible as compared to the role of potent factors such as avian malaria; 2) independent individual events tend to average out in large populations and therefore demographic stochasticity to become negligible in large populations. In our case study,
the carrying capacity of a single patch is on average ~ 600 females or pairs (Table D5: mean = 595, range = [550- 650]), well above the threshold for possible stochastic extinction (Legendre 1999). Furthermore, individual patches are connected by dispersal and therefore, the total population size was actually bigger (the carrying capacity of the whole population was roughly 600 pairs × 20 patches = 12,000 pairs). Because our simulation study is based on a total of 450 unique individual experiments (see below), two replicates are sufficient to estimate the importance of stochasticity in our analyses using both a simple linear regression and a variance component approach (using the varcomp function in R) and therefore test our assumption. The Figure S1 (Appendix S5) shows the results of the simple linear regression between metapopulation sizes (np.metapop, our response variable) obtained for each replicate. The slope of the regression is 1.0002 (SE = 0.0014, r = 0.9996, n = 450). Hence, the part of variance explained by the residuals, corresponding to stochasticity, is 1 - r² = 0.0009, i.e. 0.09%, a result very similar to the figure obtained using a variance component approach, namely 0.0005, i.e. 0.05%. These results validate our assumption that demographic stochasticity is a negligible determinant of population trajectories in the present case study.

Altogether, our simulation study was based on a total of 5 (Malaria transmission risk) × 3 (Survival to malaria infection) × 3 (Resource Distribution) × 10 (Demographic and ecological envelope) × 2 (Replicates) = 900 model runs. A flow chart describing the different components of the simulation study, including model calibration and model runs is shown in Fig. 2. MAMO and the simulation code were written in the R language, and all analyses were performed using R version 3.0.1 (© The R Foundation for Statistical Computing).

Results

‘I‘iwi post-breeding movements

Radio transmitters were attached to 27 individuals in 2003 (7 females, 14 males, and 6 juveniles) and 34 individuals in 2004 (12 females, 14 males, 8 juveniles). Four males and one female were monitored in both years for a total of 56 individual birds over both years. Thirty-five individuals (62.5%) were detected greater than 1 km from the breeding site Pua ‘Akala (the long-distance locations) during the study, for a total of 107 long-distance locations between the two years (Table 1, Fig. 1). Of the long-distance movements, 89 were detected during aerial flights, and 18 were detected during ground surveys.

The majority of long-distance movements were to areas in the northeast portion of the wet forest at mid-elevation locations (average elevation 1,390 m: see Table 1, Fig.
1), with individuals crossing through mostly contiguous wet forest from Pua ‘Akala (Fig. 1). No birds were ever detected in the remnant dry forest above 2,000 m elevation (maximum elevation = 1,990 m), although searching intensity was lower in these areas, and only two individuals were located south of the study site (Fig. 1). One was a female never located again and the other was a juvenile that was subsequently located northeast of the capture location at a later date. Most (76%) long-distance locations were found off the Hakalau Forest National Wildlife Refuge.

Visual confirmation of birds that traveled away from the breeding site was difficult due to inaccessible terrain. However, we were able to ground-track along the trail access in Laupahoehoe NAR and visually observe two different individuals with radio-transmitters. Both had nested at Pua ‘Akala in the preceding months. In June 2003, one female was seen 15.9 km to the northeast at 1,200 m elevation. A begging juvenile was heard nearby, but not confirmed. In June 2004 a female and her dependent offspring (juvenile was color marked, actively begging) were observed 16.7 km to the northeast of Pua ‘Akala at 1,090 m elevation. Both females were observed foraging in the blossoms of ‘ohi’a.

We used linear mixed-effect models to characterize the distance from breeding site and elevation of long-distance locations. Distances travelled were similar in the two years, with an average distance of 12.47 km in 2003 (± 0.51 SE) and 13.07 km in 2004 (± 0.60 SE) (t = -0.72, P = 0.47). Because long-distance locations could not be distinguished always between individuals foraging and individuals still moving, these distance estimates represent a snapshot in time. Among age classes, juveniles tended to move farther, with an average distance of 14.53 km (± 0.88 SE) versus 12.23 km (± 0.42 SE) for adults, but the difference was not significant (t = 1.42, P = 0.17). Distances traveled by adult males (12.10 ± 0.49 SE) and females (12.57 ± 0.81 SE) were similar (t = -0.48, P = 0.64), but birds travelled farther in the first part of the non-breeding season (15.07 ± 0.61 SE) than in the second (11.96 ± 0.44 SE) (t = -2.58, P = 0.01).

Altitudinal migratory birds were located well below both the seasonal maximum (1,715 m) and the year-round (1,475 m) elevations for mosquitoes as modeled by Ahumada et al. (2004) (Figs. 1 and 3). Considering all long-distance locations (n = 107), 95% were below 1,715 m and 53% were below 1,475 m. The mean elevation in 2003 of birds involved in long-distance movements (1,373 m ± 34 SE) did not significantly differ from the mean elevation in 2004 (1,410 m ± 35 SE) (t = 1.67, P = 0.10). Elevation of adult males and females were similar (t = 0.67, P = 0.51), but there was a difference between adults (1,434 m ± 26 SE) and juveniles (1,238 m ± 52 SE) (t = -2.27, P = 0.03). Elevation varied seasonally with a temporal pattern in elevation as
the summer progressed: lower elevations immediately following the breeding season in May (1,190 m ± 74 SE) and June (1,165 m ± 33 SE) compared to July (1,502 m ± 40 SE) and August (1,439 m ± 34 SE) (Fig. 3). Accordingly, elevation in the first part of the non-breeding season (nb.1, May and June) was significantly different from the latter months (nb.2, July and August) (t = 4.65, P < 0.001), but elevation in months within each non-breeding period (nb.1 and nb.2) were not significantly different (Kruskal-Wallis tests: z = 0.53, P = 0.60, z = 0.89, P = 0.37, respectively).

Altitudinal blooming pattern

Across the entire non-breeding season, forests in the Laupahoehoe study area (elevations 970–1,470 m) had significantly higher average bloom than Pu‘u ‘Akala (1,920 m) (Kruskal-Wallis test, z = -1.97, P = 0.049). However, bloom patterns for ‘ohi‘a changed considerably over time in the Laupahoehoe study area, following an altitudinal progression across the non-breeding season (Fig. 4, Appendix S1). In the early post-breeding season (May and June, nb.1), peak bloom was at 1,060 m, whereas the peak bloom was at 1,400 m in the second part of the non-breeding season (July and August, nb.2). There was a significant difference in the elevational distribution of ‘ohi‘a bloom between the two non-breeding periods in both years (2003, χ² = 103.96, df = 6, P < 0.001; 2004, χ² = 13.53, df = 6, P = 0.035). There was also a significant difference in elevational bloom pattern between years in the first non-breeding period (χ² = 44.10, df = 6, P < 0.001), but not in the second non-breeding period (χ² = 3.75, df = 6, P = 0.71).

Model

Model calibration allowed us to select a set of 10 parameter combinations (‘demographic and ecological envelope’) that produced results almost perfectly matching the observed clinal distribution of ‘ī‘īwi along the elevational gradient (Fig. 5; Appendix S4 for details). This process allowed us to eliminate some inappropriate parameter values in our simulation study, such as the high value for natal dispersal which tends to produce a stronger rescue effect at lower elevations than is actually observed (Appendix S4 Fig. S1).

Our simulation study suggests that current population size in the study area is only ~ 43.3% of the (average) estimated historic, pre-malaria carrying capacity (Fig. 6). Even in high elevation, disease-free refuge populations (> 1,715 m), current densities are ~ 13.1% below the estimated carrying capacity (Fig. 5). As expected, the negative effect of an increased malaria transmission risk from climate change strongly depends
on malaria survival. If the probability of survival from acute infection \((\text{Sm.ac})\), currently estimated at 0.13 (malaria mortality = 3 on Fig. 6), reached 0.26 in the near future (malaria mortality = 2 on Fig. 6), the prospective for ‘i‘iwi resilience to climatic change would be dramatically improved (see also Fig. 7).

Without increased survival to malaria infection, our projections suggest that ‘i‘iwi will be on the verge of extinction by 2100, given changes in disease distribution, with the total number of pairs reaching only approximately 15.2% of the estimated pre-malaria carrying capacity (Fig. 6: malaria mortality = 3, risk = 5), although the variance around this mean estimate was high (95% confidence interval = 0.3–24.6%). To identify the parameters contributing the most to the variability of future prediction, we calculated Pearson’s correlation coefficients between the predicted metapopulation size \(\text{np.metapop}\) and all the variable parameters in the calibration ‘envelope’ (Appendix S4 Table S2). All 10 coefficients were smaller than 0.49 (in absolute value) except two: \(r(\text{np.metapop}, \text{K.b}) = -0.96\) and \(r(\text{np.metapop}, \text{γ.mov}) = -0.98\). In fact, \(\text{γ.mov}\) and \(\text{K.b}\) are tightly linked in the calibration ‘envelope’ (Spearman’s rank correlation coefficient = 1), suggesting that a single factor related to migration propensity underlies the variability in future predictions. What we learn from the calibration step is that a small degree of migration propensity \((\text{γ.mov} = 0.159)\) can be coupled with a small carrying capacity \((\text{K.b} = 550)\) to produce the current pattern of ‘i‘iwi distribution along the elevational gradient (Fig. 5, pink color; Appendix S4 Table S2). Conversely, a greater degree of migration propensity (e.g., \(\text{γ.mov} = 10\)) increases the exposure to malaria and therefore mortality of migrants from high elevation. A greater carrying capacity (in this case, \(\text{K.b} = 650\)) is necessary to compensate for this extra mortality and produce the current pattern of ‘i‘iwi distribution. We currently do not have the data to distinguish between these scenarios and so both are possible. However, their implication for future ‘i‘iwi dynamics is very different. The extinction risk in 2100, as measured by the remaining metapopulation size, is strongly positively related to the migration propensity parameter (Fig. 6: light grey, mid-grey and dark grey horizontal bars correspond to \(\text{γ.mov} = 0.159, 0.541\) and 10, respectively). As expected because the total population size in the future will rely heavily on high-elevation populations, high-elevation population size will also depend strongly on the current (and future, if different) migration propensity (Fig. 7). Altogether, this suggests that for any given rate of malaria infection in the future (the actual threat), a greater degree of migration propensity will be associated with a greater population decline and an increase of extinction risk.

The importance of migration propensity suggests that changes to the distribution of resources could have significant effects on population sizes. Indeed, increasing nectar resources at high elevations (at 1,700–1,900 m) during the second period of the non-
breeding season always benefited birds at these altitudes, but also at lower elevations to roughly 1,500 m (Fig. 8). Interestingly, the expected benefit of increasing resources appears to vary as a function of the actual level of malaria transmission risk (Fig. 8). Management efforts to reduce disease prevalence, as modeled by reducing projected malaria transmission risk in 2100 by half, would contribute to buy 'i'iwi some time, but this effect is essentially restricted to higher elevations where malaria risk is lowest (Fig. 7, malaria mortality = 3, risk = 4).

**Discussion**

*The existence of current seasonal movements*

Our radio telemetry study demonstrates for the first time that breeding adults and juveniles 'i'iwi originating from an upper-elevation population at Hakalau Forest NWR (1,920 m) exhibit long-distance post-breeding movements to significantly lower elevations (Table 1, Figs 1 and 3). Two lines of evidence suggest that these movements can be explained by the tracking of 'ohi'a bloom. First, forests in the Laupahoeoe area had significantly greater bloom than Pua 'Akala based on ground measurements (Fig. 4). Second, we observed a marked temporal pattern in 'i'iwi elevation as the summer progressed: birds used lower elevations immediately following the breeding season in May and June (average of 'migrating' birds ~ 1,180 m) as compared to July and August (average ~ 1,470 m; Fig. 3). This temporal pattern in 'i'iwi elevation matched the altitudinal progression for 'ohi'a bloom in the Laupahoeoe area study area (Fig. 4, Appendix S1). In tropical systems, seasonal fluctuations in bird density have been associated with regional peaks in fruiting or flowering (Solorzano et al. 2000, Cotton 2007). Alternatively, unpredictable flowering of nectar producing trees has been associated with nomadic movements of nectarivorous birds across both large and small landscape scales (e.g., Brown & Hopkins 1996). However, because post-breeding 'i'iwi movements in response to blooming in the Laupahoeoe area were similar in 2003 and 2004, the former scenario may be more likely.

We believe that the decidedly non-random direction adopted by 'migrating' 'i'iwi (to the northeast: Fig. 1) during the two years we followed them is likely due to the patchy distribution of flowering resources, and particularly 'ohi'a, that the birds are tracking. While there are a number of flowering plant species across the Hamakua landscape, 'ohi'a strongly dominates the landscape. Fancy and Ralph (1998) reported that 'i'iwi spent more than 80% of time foraging at 'ohi'a for nectar and insects at 3 sites and not surprisingly, Hart et al. (2011) estimated that after 'ohi'a the six commoner mid-canopy tree and shrub species producing nectar accounted for only ~10% of the trees present. However, 'ohi'a does not bloom uniformly in space and time; instead, there is wide
variance in site-specific timing of flowering peaks with some plastic (e.g., based on substrate) or genetically-based spatial variation (e.g. Cordell et al. 1998, Berlin et. al 2000, Hart et al. 2011). On Maui Island, Berlin et al. (2000) documented two varieties of 'ohi'a which peaked in different months. Pubescent 'ohi'a flowered annually, peaking in fall and winter, and because of its relative abundance, determined the overall pattern for the species, while the less abundant glabrous 'ohi'a had a high peak from April through June. In our study, observations from low-altitude airplanes during radio tracking provided the general impression that 'ohi'a bloom was concentrated in the northeast section of the forest. Individual trees with elevated bloom (>30% crown covered in blossoms) can be seen from the air, and during tracking flights, 'ohi'a with elevated bloom were only seen in the northeast section, where as much as 70% of the canopy was covered in blossoms (Kuntz 2008). Conversely, 'ohi'a trees in the rest of the study area showed little bloom during the summer months that 'i'iwi were tracked (e.g., maximum in Pua 'Akala was 25%). 'I'iwi appears to specialize on high-quality resources, as it spends the majority of its time exploiting resources on trees that have a high number of flowers, only very rarely feeding on trees with small numbers of flowers (Pimm and Pimm 1982). Hence, our observation that 'i'iwi focused on the northeast of the study area is consistent with the hypothesis that it is seeking out the highest quality patches available. Future research should examine whether the variability in 'ohi'a bloom on Mauna Kea is associated with different substrate or varieties, and determine how predictable blooming patterns are across time.

While 'ohi'a is clearly an important tree for 'i'iwi, other flowering plants certainly play a role on the distribution and movements of 'i'iwi. 'I'iwi will feed on a variety of other nectar sources including native shrubs and trees such as māmane, as well as introduced species which offer abundant nectar such as banana poka (Passiflora mollissima) (Scott et al. 1986). Seasonal abundance of 'i'iwi in high elevation dry forests is related to the intensity of māmane bloom (Hess et al. 2001), although we did not detect movement to higher elevation forests despite regular searches of the māmane forest above Hakalau (Kuntz 2008). However, peak bloom season for māmane (September–December) is outside the period of time that we tracked 'i'iwi, and seasonal upslope movement may occur but was not documented by this study. Since these movements would be to areas where disease does not currently occur, they are not likely to have the same implications for population dynamics as down-slope movement to areas where disease transmission is high.

The rich nectar of the introduced vine banana poka attracts many birds, including 'i'iwi, for which the vine can provide a major source of nectar locally and may attract 'i'iwi from afar where abundant. Banana poka used to be abundant in Laupahoehoe forest, with a bloom peak during 'i'iwi’s non-breeding season from May to August (La
Rosa 1984), but banana poka was widely suppressed from biocontrol at the time of our study (2003–2004). Four years after the field inoculations of the biological control agent *Septoria passiflorae*, which occurred in 1996–1997, reduction reached more than 95% almost everywhere, including Laupahoehoe (Trujillo 2005). As a result, banana poka was not present in large amounts across the landscape (although it could still be abundant in localized areas) and incidental field observations in Laupahoehoe (2003-2004) suggested that radio-tagged birds were foraging primarily in ‘ohi’a bloom (Kuntz 2008). Although abundant poka may once have been an important driver of ʻiʻiwi’s movements around Laupahoehoe, the fact that their movement patterns were similar two years in a row after poka had been suppressed (in 2003 and 2004: Fig. 1) indicates that they were finding suitable habitat and resources despite poka’s suppression.

Altogether, ʻiʻiwi appears as a flexible and adaptable species. This is demonstrated by the historical switch from Hawaiian lobelioids to ʻohi’a (Smith et al. 1995), its capacity to take advantage of persisting native shrubs such as ʻākala (*Rubus hawaiensis*: in Maui, 22% of foraging observations on flowers were on ʻākala, versus 57% for ʻohi’a; Berlin et al. 2001), and emerging invasive species such as banana poka in Hawai‘i and tree alfalfa (*Cytisus palmensis*) in Maui (Fancy and Ralph 1998). Accordingly, ʻiʻiwi certainly maximized blooming opportunities when visiting the northeast section of our study area, which included residual banana poka, and the gradual use of higher-elevation habitats as summer progressed was a dynamic response to the geographic changes in the bloom of ʻohi’a as well as, probably, other native or non-native plants with similar phenology. As restoration efforts produce areas with more diverse nectar resources, the movement patterns of ʻiʻiwi may shift to account for a more varied resource landscape. Future studies of actual use of the various nectar sources could be performed in comparison with their relative abundance and energetic content, including potential synergistic effects between ʻohi’a and other native or invasive plants.

While we observed seasonal movement in ʻiʻiwi on the Hamakua Coast, observations of large scale movement across the species’ range were once frequently noted, but not in recent times. There are several possible explanations for the lack of recent observations of large-scale altitudinal movement in ʻiʻiwi (and ʻapapane). The hypothesis that nectar resources are not a limiting factor anymore after the extinction of larger endemic nectarivores does not appear to be supported, as we have documented that an altitudinal migration system still exists for ʻiʻiwi. Alternatively, the ecological trap scenario where individuals from a population with a higher propensity to follow flowering peaks into malaria-affected areas may have been selected against in favor of more sedentary individuals is not fully supported, but could be contributing to the
pattern of 'i'iwi movement. First, lower elevations (between 1,000 and 1,200 m) are visited during the period when the malaria transmission risk is the lowest (Fig. 1; Appendix S2), which could favor the sustainability of these migrations. Second, 'i'iwi rarely are detected in low elevation forest below ~ 1,000 m, regardless of the bloom intensity (WAK personal observation; see also Fig. 1). This seems surprising given 'i'iwi readily move from high elevations to mid-elevations, the forest is relatively contiguous from high to low elevations (Fig. 1), and low elevation 'ohi'a tend to have significantly more bloom for longer periods of the year than higher elevation trees (Hart et al. 2011). Possible explanations could include recent and ongoing selection over the last decades caused by malaria mortality that has favored less mobile, higher elevation individuals. Alternatively, there may be sufficient resources at mid and high elevations, especially when one considers that introduced avian diseases and other threats have largely depleted the native populations of nectarivores, such as 'i'iwi, at mid and low elevations (Fig. 5). Nonetheless, our research clearly shows that altitudinal migration persists to present days, but may not occur at levels once observed due to diminished populations and far more fragmented landscapes (but note that forests in the study area remain largely unfragmented: Fig. 1).

**Interactions between seasonal movements, avian malaria and climate change**

As a consequence of their post-breeding movement well below both the mosquito self-sustaining (1,475 m) and summer (1,715 m) range limits, 'i'iwi individuals experienced a higher probability of exposure to avian malaria than more sedentary species which remain in the high-elevation disease-free zone (Appendix S2). Our spatial, individual-based model produced a number of important conclusions concerning the current and future impact of avian malaria and its interactions with seasonal downslope movements on the 'i'iwi.

First, by simulating pre-malaria conditions on 'i'iwi abundance in the upper half of the elevation gradient (950–1,950 m) of the Hamakua region of Hawaii Island, we estimate that 'i'iwi populations at these elevations have been more than halved since the introduction of malaria (~ 43.3% remaining). Because 'i'iwi were previously present in the lower half of the elevation gradient (0–950 m), where 'ohi'a flower density and nectar production tend to be higher than in high-elevation forests (Hart et al. 2011), we can infer that only ~ 43.3 / 2 = 21.6% of total pre-malaria 'i'iwi numbers persist in mesic and wet forests of Hawai'i island today (assuming the same historical number of 'i'iwi in the lower and upper sections of the gradient). Even in refuge populations higher than 1,715 m, where the chance of being infected by malaria is currently low (Ahumada et al. 2004, Samuel et al. 2015, Appendix S2), breeding densities fail to reach the estimated carrying capacity. Two factors certainly contribute to the reduced population
size (approximately 13%; Figs. 5, 7): 1) the existence a seasonal 'migration load', with some high-elevation breeding birds moving to lower-elevation habitat during the non-breeding season, contracting malaria and dying; and 2) a deficit of low-elevation immigrants dispersing into high-elevation patches due to reduced population sizes in lower elevations with high avian malaria mortality.

Second, if we base our conclusions on the current estimate for malaria mortality, our projections suggest that `i`iwi will be on the verge of extinction in 2100, with the total number of pairs in our study area (at elevations of 950–1,950 m) reaching only 0.3–24.6% of the estimated carrying capacity (mean = 15.2%: Fig. 6). This corresponds approximately to 0.2–12.3% of pre-malaria numbers (considering populations across the whole elevation gradient), even though the emission scenario used for the downscaled climate models (RCP4.5) is optimistic. Daily malaria infection rates for alternative global climate change scenarios (A1B and RCP8.5) are predicted to be considerably higher because these alternatives have either higher rainfall and similar temperature increases (A1B) or lower rainfall and higher temperature increases (RCP8.5) (Liao et al. 2015).

As a result, the remaining pairs will be found at increasingly higher elevations. The median elevation of `i`iwi pairs in the study area (950–1,950 m) shifted from 1,450 m in the pre-malaria era, to 1,688 m currently and 1,762 m in 2100 (not shown; but see Fig. 5). The upper elevation of the forest is capped by the trade-wind inversion (TWI; Diaz et al. 2011) which limits precipitation above 2,000–2,500 m. The continuation or strengthening of the TWI, a predicted consequence of climate change (Cao 2007, Timm and Diaz 2009), reduces the likelihood of a gradual shift of rainforests towards higher elevations, which would effectively dampen the decline we modeled, at least temporarily.

We identified two parameters whose knowledge will be critical to increase the accuracy of possible trajectories of `i`iwi in the future, specifically malaria mortality \(Sm.ac\) and migration propensity \(\gamma.mov\). A priority for future research is to better understand the spatial and temporal variation in the rates of malaria infection (see above) and mortality which combine to drive population mortality. Assuming other calibration parameters remain constant, even a relatively modest improvement in `i`iwi’s current probability of malaria survival (0.26, compared to the current estimate of 0.13), could yield a dramatic increase in the viability of `i`iwi (Figs. 6–7). For comparison, a malaria survival rate of 0.26 is still lower than rates documented for `Apapane and Hawai`i `amakihi populations which have persisted at mid-elevations and lower (Samuel et al. 2015). This suggests, given the results of our model, that species such as Hawai`i `Amakihi that have evolved increased tolerance to malaria will fare much better in the
coming decades compared to ‘i’iwi (see also Liao et al. 2015). However, there is great uncertainty in future climate conditions, and thus malaria intensity at different elevations. Elucidating the genetic underpinning of malaria resistance and tolerance in ‘i’iwi and closely related species would offer the opportunity to predict future development of genetic resistance/tolerance of ‘i’iwi populations over time within our modeling framework (see also Kilpatrick 2006 for a simple model).

The probability of extinction of ‘i’iwi populations, as measured by population estimates for 2100, is also related to their propensity to seasonally track abundant nectar sources. Higher estimates of migratory movements across the landscape ($\gamma$.mov) produce the most pessimistic scenarios of decline because birds move to lower elevations with higher malaria infection risk (Fig. 6). A formerly adaptive behavior certainly has the potential to become maladaptive in the new, modified environment, providing yet another mechanism by which specialists could be facing higher extinction risks under rapid environmental change (e.g., Colles et al. 2009). While our knowledge of ‘i’iwi movement patterns is currently rudimentary, future telemetry studies combined with bloom surveys along the elevational gradient would allow refinement of the migratory movement parameter. Together with improved estimates of carrying capacity based on the distribution and abundance of resources, these data could help reduce an important fraction of the current uncertainty in population trajectories towards 2100.

**Management strategies**

Effective conservation of mobile species requires developing management strategies at the appropriate geographic scale. Many tropical species rely on seasonal changes in fruiting or flower phenology (Powell & Bjork 2004). In the Hawaiian rainforest, nectarivorous species may not rely on regional habitat diversity, since ‘ohi’a is the primary rainforest canopy tree, but on the temporal/spatial distribution of nectar availability. Continued landscape-level access to seasonally variable nectar resources may be critical for long-term population persistence of ‘i’iwi and ‘apapane (Ralph & Fancy 1995).

Our preliminary assessment of two potential mitigation actions suggests that only a multi-pronged response is likely to succeed given the complexity of threats impacting the ‘i’iwi. Given the fragility of Hawaiian ecosystems, new threats may emerge anytime, such as the recently described pathogen, a *Ceratocystis* Wilt, believed to be responsible for extensive ‘ohi’a mortality during the past five years (Keith et al. 2015). Using our model (MAMO) we assessed the potential benefit of halving malaria transmission projected in 2100. A halving of the malaria risk might be achieved through an ambitious program of feral pig control throughout the refuge (currently only in upper portions), as
their foraging habit is responsible for the creation of standing water sources suitable for mosquito breeding (LaPointe et al. 2009, Hobbelen et al. 2012). While we found that management aimed at reducing transmission risk would indeed contribute to buy 'i'iwi some time (Figs. 5–7), we observed that this effect is essentially restricted to higher elevations (Fig. 7). At mid (~1,500 m) and especially, low (~1,200 m) elevations, such a considerable effort (dividing the risk by two) would not reduce the risk of extinction, as the annual probability of becoming infected for 'resident' 'i'iwi rapidly tends towards 1 (at 1,500 m, \( P \approx 0.65 \) for '2100/2', \( P \approx 0.88 \) in 2100; at 1200 m, \( P \approx 1 \) for '2100/2' onwards). These findings are in agreement with previous work that suggested vector populations must be brought down to very low levels (80–95% reduction) to break the disease cycle (Samuel et al. 2011, Hobbelen et al. 2012). While it therefore might seem tempting to restrict management to higher elevations, we stress that the transitory benefit observed at high elevations (for '2100/2': see Fig. 7, top) depends at least in part on the reduction of malaria prevalence at lower elevations, as it directly benefits seasonal migrants coming from the higher elevations.

Second, we tested the hypothesis that by providing a higher level of nectar resources at high elevations (≥ 1,700 m), we could limit the negative consequences of seasonal movement for 'i'iwi. This strategy could theoretically be achieved by differentially altering the proportion of nectar-producing species or ecotypes with the appropriate phenology at different elevations: 1) decreasing their proportion in malaria-infested areas, focusing on eradication of invasive species that produce nectar, such as banana poka; and simultaneously: 2) increasing native flowering plants in high-elevation areas, either via outplanting or by facilitating natural regeneration through population control of introduced ungulates. In particular, the foraging behavior of pigs may reduce the amount of nectar produced by understory plants such as 'ākala (Nogueira-Filho et al. 2009), which blooms during 'i'iwi's non-breeding season (in summer). Since its inception in 1986, Hakalau Forest NWR has been actively restoring upper elevation forests through a combination of ungulate control, reforestation, and outplanting native understory plants, which has increased understory diversity. However, the recovery is slow, and limited to upper portions of the refuge, and novel approaches such as the use of artificial feeders may be an appropriate surrogate while habitat restoration is underway. Artificial feeders are readily used by avian nectar specialists across the globe (such as hummingbirds in the Neotropics, sunbirds in Africa and honeyeaters in Australia: e.g., Armstrong 1992, Downs and Perrin 1996), and have been successfully used to increase resource availability for the Hawaii Amakihi (van Riper 1984). The adaptability of 'i'iwi to new nectar sources and its capacity to explore high-elevation māmane forests suggest that artificial feeders placed in disease-free habitats may be a promising tool for 'i'iwi management and conservation. While the
magnitude of the potential effect may be relatively modest, at least within the bounds of our virtual experiment design (Fig. 8), supplementing nectar resources could be implemented in combination with other practices to buy ‘i‘iwi some time. Interestingly, a positive impact of supplementing resources was observed beyond the managed area itself. First, a greater fraction of e-birds breeding at mid-elevations (1,500–1,600 m) migrated to higher-elevations patches during the second part of the non-breeding season, thereby reducing the risk of being infected. Second, greater survival at high elevation may have favored lower patches through a source-sink dynamics (rescue effect).

Management strategies for maintaining ‘i‘iwi populations have historically been focused on the preservation of native mesic and wet forests, reforestation and control of feral ungulates in upper elevation breeding sites, such as those that occur on Hakalau Forest National Wildlife Refuge. However, the high degree of movement in ‘i‘iwi highlights the importance of land managers working across jurisdictional boundaries, since the majority of long-distance records were off the refuge (Fig. 1). Because movement brings ‘i‘iwi to areas where disease transmission is high, partnerships are needed that protect and manage areas necessary for all stages of their annual cycle. This is not unique to Hawaii, but throughout the tropics where breeding habitat is located in reserves, but non-breeding habitat is not adequately protected (e.g., Chaves-Campos et al. 2003; Powell & Bjork 2004). In addition to the management of low-elevation post-breeding areas, the control of ungulates and reforestation of higher elevation areas currently beyond the tree limit with drought-resistant species or ecotypes should be considered. Such a strategy could help buy time for ‘i‘iwi populations even if gradual shift of wet rainforests towards higher elevations does not occur naturally in response to climate change due to the strengthening of the trade-wind inversion.

The greatest increase in population size came with reduced susceptibility to malaria in ‘i‘iwi. To facilitate evolution of disease resistance, managers can work to keep populations as large as possible for as long as possible. For example, habitat restoration could increase the carrying capacity of an area, providing a larger gene pool for natural selection to work on. Additionally, actions that could increase productivity (habitat restoration, nest predator control) could partially offset the increased mortality from disease, allowing for a slower population decline that buys more time for birds to potentially evolve immunity (Kilpatrick 2006).

Model assumptions and future directions

Our model relies on a number of assumptions and simplifications which influence
conclusions. In particular, our model is female-based. While on one hand female ‘i‘iwi may be subjected to higher rates of malaria infection given their higher proportion of time away from high elevation sites (presumably to low-elevation sites during the non-breeding season; Kuntz 2008), males may actually be more susceptible than females (Atkinson et al. 1995); how exactly these two factors balance is currently unknown. Second, while we assumed breeding parameters such as beginning and duration of the breeding season to be constant across elevation (Appendix S4), they might actually differ to some extent in response to differential ‘ohi‘a phenology (see Appendix S1). Third, we assumed that breeding dispersal was not affected by local breeding success or density-dependent factors, and density-dependent natal dispersal only depended on local densities. If low-elevation patches tend to be attractive to dispersing individuals because of a lack of apparent competition and abundance of available resources, an accelerated population collapse could be anticipated because of the greater exposure of low-elevation patches to malaria (ecological trap). Conversely, because density tends to be correlated to patch reproductive success (Doligez et al. 2004), low-elevation patches may be actively avoided by dispersing individuals because of the absence of social cues. Furthermore, we assumed no penalty for dispersal, but dispersal can be costly by increasing mortality (Bonte et al. 2012). Fourth, the form of density regulation was assumed to be known (Appendix S3) and was therefore not subjected to calibration. This assumption could be released in future versions of the model since the form of density regulation may influence population trajectories (Saether and Engen 2002).

Despite the necessary simplifications, we believe that our simulation outputs can be regarded as credible inferences. Our approach of calibrating the model parameters to an independent dataset (abundance of ‘i‘iwi along an elevational gradient) allowed us to reject some parameter values that could have been regarded as legitimate based on available literature (e.g., Appendix S4 Fig. S1). Of course, only a small fraction of the parameter space was explored during the calibration process, and we can expect a large number of parameter combinations yielding similar results (undetermined system). Nonetheless, this approach provided a model that represents the observed system very well (Fig. 5). Furthermore, the use of our calibration ‘envelope’ allowed us to intrinsically account for demographic and environmental uncertainty in future predictions, by averaging across 10 different best models. We did not explicitly incorporate environmental stochasticity into our model, instead focusing on the average effects of changing conditions and alternative management actions on population dynamics. For instance, heavy rains can depress productivity of Hawai‘i forest birds (Cummins et al. 2014), and warm, wet conditions can produce epizootic events that increase mortality from disease in some years (Atkinson and LaPointe 2009). Conversely, years that are drier or cooler than normal will have lower nest failure or
disease mortality, and over time these unpredictable stochastic events will produce an average effect that shapes the distribution and abundance of the birds across the landscape to which our calibration 'envelope' was fitted to. Nevertheless, future modeling could explicitly consider the effects of environmental stochasticity as it may increase the chances of stochastic extinction (Lande 1993). In addition, new studies including fieldwork to improve the knowledge of critical model parameters such as migration propensity, habitat carrying capacity and future malaria infection rates (see above) will be important to reduce the current uncertainty in population trajectories.

Many parameters influence species dynamics, and their potential interactions are too complex for simple intuition. Following the recommendations of a structured decision making workshop aimed at identifying and prioritizing conservation actions to address the threat of climate change on Hawaiian native forest bird community (Paxton et al. 2011), our model can help predict possible outcomes of management actions while accounting for changing environments, such as increasing elevation of avian malaria transmission over time. Furthermore, our preliminary simulations provide support to the view that MAMO can be a cost-effective management tool capable of optimizing not only management actions but also the timing for their implementation. For instance, we showed that the expected benefit of increasing nectar resources at high elevations depended on the actual level of malaria transmission risk (Fig. 8). An immediate implementation of the management to increase nectar resources is predicted to have only a minimal impact on 'i'iwi populations. Formal benefit-cost ratio analyses may be implemented in the future to make MAMO a comprehensive Decision Support Tool. Our model is general and flexible, and could ultimately be applied to a whole suite of other species and ecosystems in Hawaii and beyond. A community-level version of MAMO is currently under development.

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Literature Citations


Paxton, E. H., P. M. Gorresen, and R. J. Camp. 2013. Abundance, distribution, and population trends of the iconic Hawaiian Honeycreeper, the 'I'iwi (Vestiaria


Warner, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70:101–120.


Data Availability Statement

All the code (in the R language) and data sets needed to replicate the simulations presented here are available at http://doi.org/10.5281/zenodo.251368. Movement locations have been deposited in DRYAD (doi:10.5061/dryad.442r8).
Tables

**Table 1** Distance and elevation of radio telemetered ‘i’iwi detected greater than 1 km from capture site (Pua ‘Akala, 1,920 m). For each group (adult females, adult males, and juveniles of unknown sex), out of the total number telemetered birds (n.i), a subset (n.i > 1) was detected greater than 1 km from the capture location. We also present the total number of locations greater than 1 Km for each group (n.loc > 1). For the long distance detections (n = 107), we present the average distance (avg.dist) in Km from Pua ‘Akala together with the standard deviation (± SE), the average of the farthest distance per individual (avg.farthest), the farthest distance (farthest.dist), the average elevation (avg.elev) in meters above sea level, the average of the lowest elevation per individual (avg.lowest), and the lowest elevation (lowest).

<table>
<thead>
<tr>
<th></th>
<th>Groups</th>
<th>n.i</th>
<th>n.i&gt;1</th>
<th>n.loc&gt;1</th>
<th>avg.dist</th>
<th>avg.farthest</th>
<th>farthest.dist</th>
<th>avg.elev</th>
<th>avg.lowest</th>
<th>lowest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult females</td>
<td>19 10 (53%) 22</td>
<td>0.81</td>
<td>1.23</td>
<td>17.88</td>
<td>14.12 ±</td>
<td>12.57 ±</td>
<td>12.10 ±</td>
<td>48</td>
<td>1297 ± 74</td>
<td>1013</td>
</tr>
<tr>
<td>Adult males</td>
<td>28 14 (50%) 61</td>
<td>0.49</td>
<td>0.69</td>
<td>18.31</td>
<td>15.06 ±</td>
<td>14.53 ±</td>
<td>15.06 ±</td>
<td>31</td>
<td>1237 ± 54</td>
<td>820</td>
</tr>
<tr>
<td>Juveniles</td>
<td>14 11 (79%) 24</td>
<td>0.88</td>
<td>1.10</td>
<td>19.64</td>
<td>15.71 ±</td>
<td>14.53 ±</td>
<td>19.64 ±</td>
<td>52</td>
<td>1192 ± 81</td>
<td>738</td>
</tr>
<tr>
<td>Overall</td>
<td>61 (57%) 107</td>
<td>0.39</td>
<td>0.56</td>
<td>19.64</td>
<td>15.00 ±</td>
<td>12.74 ±</td>
<td>12.74 ±</td>
<td>25</td>
<td>1240 ±</td>
<td>738</td>
</tr>
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</table>
Figure 1. Geographic distribution of radio telemetered 'i'iwi detected greater than 1 km from capture location, Pua 'Akala (green square). Locations were based on aerial and ground tracking, with estimated error of up to 1 km (represented by dash yellow circle). Many of the birds left Hakalau Forest NWR (orange lines) to move north to Laupahoehoe Forest Reserve and Natural Area Reserve lands (blue line), or even further north. 'Ohi'a bloom was measured along an elevation transect between 970–1,470 m (indicated by green dots), and at the Pua 'Akala site (1,920 m). Elevation contours are shown for 500 m increments. Shades of green represent wet-mesic and montane forest types, with dark green = closed canopy forest; medium green = open forest canopy, and yellow-green = representing sparse, boggy forest.
Figure 2. Flow chart describing the different components of a typical simulation study based on the model MAMO, including model calibration and model run.
Figure 3. Mean elevation (± 1 SE error bars) of radio tracked ‘i‘wi for each non-breeding period (nb.1 = May and June, nb.2 = July and August) and the two years (2003 and 2004). Only the birds detected farther than 1 km from the capture location are included.
Figure 4. Average ‘ohi’a bloom (2003 and 2004 combined) by elevation for May and June (nb.1, black bar) and July and August (nb.2, grey bar). Stations were sampled in the Laupahoehoe Natural Area, except at 1,920 m (Pua ‘Akala breeding site).
Figure 5. 'I'iwi distribution along the elevational gradient. Predicted 'I'iwi density (# pairs ha^{-1}) is plotted for pre-malaria (light grey), present (pink), current malaria transmission risk / 2 (medium grey), and future climatic conditions (dark grey = malaria transmission risk in 2100 / 2, black = 2100). Individual squares are simulated data points, thin dashed lines are sigmoid clines fitted for individual simulation run, and broad dashed lines are sigmoid clines fitted for average population size at each elevation during the corresponding period. The observed current 'I'iwi population size is shown by red crosses and the solid red sigmoid curve. Only simulations corresponding to the current level of malaria mortality (AC = 3, i.e. Sm.ac = 0.13) and resources during the second period of the non-breeding season (RES = 1, i.e. no supplementation) are included.
Figure 6. Total number of pairs of ʻiʻiwi in the metapopulation. The study area comprises a total of 20 square patches of 1 km$^2$ each spread onto ten 100 meter-each elevational bands (2 patches per elevation). Patch centers range from 1,000 to 1,900 m. The x-axis represents the probability to die from malaria infection (malaria mortality = 1 - Sm.ac): 1 = 0.61, 2 = 0.74, 3 = 0.87 (current estimate) as a function of malaria transmission risk: 1 = Pre-malaria (transmission risk null), 2 = current risk / 2, 3 = Present, 4 = risk in 2100 / 2, 5 = risk in 2100. The observed current ʻiʻiwi population size is shown by a grey cross. Simulations are shown in open symbols (filled symbols = simulation averages, connected by lines). In addition, for malaria mortality = 3 and risk = 5 (bottom right) we show the range of metapopulation sizes obtained when $\gamma_{\text{mov}} = 0.159$ (small propensity to migratory movements; 2 horizontal light grey bars), $\gamma_{\text{mov}} = 0.541$ (2 mid-grey bars), and $\gamma_{\text{mov}} = 10$ (no resistance to migratory movements; 2 dark grey bars). Only simulations corresponding to the current level of resources during the second period of the non-breeding season (RES = 1) are included.
Figure 7. Differential dynamics along the elevational gradient. The $y$-axis shows the predicted number of `i`iwi pairs in a single 1 km$^2$ patch at 1,800 m (top), 1,500 m (middle) and 1,200 m (bottom). The $x$-axis represents the probability to die from malaria infection (malaria mortality = 1 - Sm.ac): 1 = 0.61, 2 = 0.74, 3 = 0.87 (current estimate) as a function of malaria transmission risk: 1 = Pre-malaria (risk null), 2 = current risk / 2, 3 = Present, 4 = risk in 2100 / 2, 5 = risk in 2100. The observed current `i`iwi population size is shown by a grey cross. Simulations are shown in open symbols (filled symbols = simulation averages, connected by lines). In addition, for malaria mortality = 3 and risk = 5 at 1,800 m we show the range of predicted number of `i`iwi pairs obtained when $\gamma$.mov = 0.159 (small propensity to migratory movements; 2 horizontal light grey bars), $\gamma$.mov = 0.541 (2 mid-grey bars), and $\gamma$.mov = 10 (no resistance to migratory movements; 2 dark grey bars). Only simulations corresponding to the current level of resources during the second period of the non-breeding season (RES = 1) are included.
Figure 8. Effect of our virtual management experiment - increasing nectar resources at high elevations (1,700 to 1,900 m) during the second period of the non-breeding season (nb.2). Predicted 'i'iwi density (# pairs ha\(^{-1}\)) is plotted for present, future (2100), and transitory (called '2100/2') climatic conditions as a function of the level of resources at high elevations: black = no change as compared to present, medium grey = 1.5 times mores bloom at high elevations than present, light grey = 2 times mores bloom at high elevations than present. Lines are sigmoid clines fitted for the corresponding treatment, after averaging individual simulation run to obtain a single average population size at each elevation. Only simulations corresponding to the current level of malaria mortality (AC = 3, i.e. Sm.ac = 0.13) are included.