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Oak habitat recovery on California's largest islands: scenarios for the role of corvid seed dispersal

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Running title: Modelling seed dispersal effects on oak expansion

Abstract

1. Seed dispersal by birds is central to the passive restoration of many tree communities. Reintroduction of extinct seed dispersers can therefore restore degraded forests and woodlands. To test this, we constructed a spatially-explicit simulation model, parameterized with field data, to consider the effect of different seed dispersal scenarios on the extent of oak populations. We applied the model to two islands in California's Channel Islands National Park (USA), one of which has lost a key seed disperser.

2. We used an ensemble modelling approach to simulate island scrub-oak (*Quercus pacifica*) demography. The model was developed and trained to recreate known population changes over a 20-year period on 250-km^2 Santa Cruz Island, and incorporated acorn dispersal by island scrub-jays (*Aphelocoma insularis*), deer mice (*Peromyscus maniculatus*) and gravity, as well as seed predation. We applied the trained model to 215-km^2 Santa Rosa Island to examine how reintroducing island scrub-jays would affect the rate and pattern of oak population expansion. Oak habitat on Santa Rosa Island has been greatly reduced from its historical extent due to past grazing by introduced ungulates, the last of which were removed by 2011.

3. Our simulation model predicts that a seed dispersal scenario including island scrub-jays would increase the extent of the island scrub oak population on Santa Rosa Island by 281% over 100 years, and by 544% over 200 years. Scenarios without jays would result in little expansion. Simulated long-distance seed dispersal by jays also facilitates establishment of discontinuous patches of oaks, and increases their elevational distribution.

4. *Synthesis and applications*. Scenario planning provides powerful decision support for conservation managers. We used ensemble modelling of plant demographic and seed dispersal processes to investigate whether the reintroduction of seed dispersers could provide cost-effective means of achieving broader ecosystem restoration goals on California's second-largest

island. The simulation model, extensively parameterized with field data, suggests that re-establishing the mutualism with seed-hoarding jays would accelerate the expansion of island scrub-oak, which could benefit myriad species of conservation concern.

Keywords: *Aphelocoma insularis*, Corvidae, Habitat Restoration, *Quercus pacifica*, Scatter-Hoarding, Scenario Planning, Seed Dispersal Mutualism, Simulation Modelling

Introduction

The spatial distribution of seeds sets the template for community structure, making seed dispersal central to plant ecology, ecosystem dynamics, and habitat restoration (Levine & Murrell, 2003). Seed movement by abiotic mechanisms, such as wind or water, has been extensively studied and modeled over the last decades (Nathan et al., 2008). However, we lack a similar understanding of seed dispersal by animals, or zoochory (Cousens et al., 2010). Predicting how animals shape the landscape through their distribution of seeds requires process-based models that capture proximate drivers of seed-related animal behavior and movement. Because animal movement and foraging behavior are dependent on the spatial and temporal distribution of resources, models that investigate animal seed dispersal need explicit links between individual-, population-, and landscape-level plant demography, seed production, and their effect on seed dispersers (Côrtes & Uriarte, 2013). Restoration strategies for ecosystems dominated by animal-dispersed plants must therefore consider interactions between plants and animals (Peterson, Cumming & Carpenter, 2003; McAlpine et al., 2016), particularly the role of seed dispersal mutualisms in achieving restoration goals (Kaiser-Bunbury, Traveset & Hansen, 2009).

Restoration of forests and woodlands can benefit from incorporating plant – animal mutualisms into management plans. These communities are often characterized by interactions between large-seeded plant species and their generalist seed dispersers (McConkey et al., 2012). Scatter-hoarding birds in the family Corvidae (jays, crows, ravens, nutcrackers, and magpies) are an iconic example of such a generalist disperser. Corvids disperse large-seeded trees, especially oaks (*Quercus* spp.) and pines (*Pinus* spp.), into both new areas and degraded habitat, and thereby maintaining gene flow among disjunct tree populations (Pesendorfer et al., 2016a). These services facilitate the abiotic and biotic conditions necessary for functioning woodland ecosystems, and have been shown to save substantial human labor costs required for seed planting (Hougner, Colding, & Soderqvist, 2006). Re-establishing such ecological connectivity by restoring habitat can reduce the effects of habitat fragmentation and reduce long-term rates of species extinctions (Newmark et al. 2017). Restoration plans for forests and woodlands should thus consider the role of scatter-hoarding animals, particularly bird species that enable long-distance seed dispersal.

Oak habitat on the two largest islands in the California Channel Islands archipelago, Santa Cruz and Santa Rosa (Fig. 1), provides a model system to evaluate the potential outcomes of habitat restoration in the presence or absence of seed dispersal mutualisms. Livestock ranching and foraging by non-native ungulates over 150 years greatly reduced the islands' native woody vegetation cover, resulting in extensive soil loss, large areas of bare ground, and widespread, non-native annual grasslands (Minnich 1980; Van Vuren & Coblentz, 1987; Rick et al., 2014). Although introduced ungulates have now been removed, the recovery of woody vegetation differs dramatically between the two islands. This difference may be due in part to the timing of the ungulate removals and to the spatial extent of the remnant oak stands, and to differences in the seed disperser communities on the islands (Morrison et al., 2011).

Specifically, the endemic island scrub-jay (*Aphelocoma insularis*), a medium-sized scatter-hoarding corvid and dominant long-distance disperser of large seeds, is currently only found on Santa Cruz Island, where it likely has been important in the rapid recovery of oak populations (Dahlin, Asner & Field, 2014; Pesendorfer et al., 2016b). Island scrub-jays are suspected from archeological excavation to have occurred on Santa Rosa Island until the late Pleistocene or early Holocene, and they may have been extirpated as recently as the late 1800s due to direct and indirect effects of sheep grazing (Collins, 2009; Morrison, 2014). The current extent of oak chaparral and woodland on Santa Rosa Island is substantially less than the area theoretically suitable for these habitats (Kindsvater, 2006). A full recovery of the island's oak habitat using manual and likely small-scale restoration efforts will take considerable time (Knapp, 2010). A proposed reintroduction of island scrub-jays to Santa Rosa Island, however, would reestablish a seed dispersal mutualism, and could accelerate recovery of the island's oak populations (Morrison et al., 2011; Sillett et al., 2012; Morrison, 2014; Pesendorfer et al., 2016b).

Here, we use a spatially-explicit simulation model to evaluate the effectiveness of island scrub-jays for oak restoration on Santa Cruz and Santa Rosa Islands. The model focuses on the endemic island scrub oak (*Q. pacifica*), the dominant oak species in chaparral on the Channel Islands (Junak et al., 1995), and includes parameters for plant demography, seed predation and dispersal. We model oak population expansion on both islands under scenarios with and without seed dispersal by jays to address three objectives. First, we use Santa Cruz Island to train the model by comparing the documented oak distribution in 1985, just before sheep were eradicated from most of the island, with the modeled and documented distributions in 2005. Second, we use Santa Rosa Island to test the hypothesis that scatter-hoarding by island scrub-jays accelerates oak population expansion compared to seed dispersal by gravity and mice. Finally, we discuss the value of the simulation model for scenario planning (Peterson et al., 2003) and for assessing how dispersal mutualisms benefit habitat restoration strategies.

Materials and Methods

Study System

Located 40 km south of Santa Barbara, California, Santa Cruz Island (34.02° N, 119.76° W) and neighboring Santa Rosa Island (33.98° N, 120.09° W) are part of the northern Channel Islands archipelago of four islands aligned along an east-west axis (Fig. 1). The islands have a mediterranean climate with cool, wet winters and hot, dry summers, and receive considerable moisture input from fog (Fischer et al., 2016). The vegetation is characterized by coastal sage scrub, oak-dominated chaparral and woodlands, and non-native grasslands (Junak et al., 1995; Cohen et al., 2009).

Conservation management on Santa Cruz Island was initiated in 1978 by The Nature Conservancy (TNC), the majority land-owner, and by the National Park Service (NPS) with the establishment of Channel Islands National Park in 1980. Removal of sheep (*Ovis aries*) between 1981 and 1999, cattle (*Bos taurus*) in 1988, and pigs (*Sus scrofa*) by 2007 facilitated passive recovery of coastal sage scrub and chaparral vegetation (Klinger, Schuyler, & Sterner, 2002; Faulkner & Kessler, 2011; Morrison, 2011; Beltran et al., 2014; McEachern et al. 2016). Spatial structure of the recovering vegetation alludes to the role of two key seed dispersers: the island fox (*Urocyon littoralis*), a generalist disperser of small-seeded, fruiting shrubs like manzanita

(*Arctostaphylos* spp.) and toyon (*Heteromeles arbutifolia*), and the island scrub-jay, an oak mutualist currently restricted to Santa Cruz Island (Dahlin et al., 2014).

Santa Rosa Island was integrated into Channel Islands National Park in 1986 but used for commercial ranching and hunting operations for an additional 25 years. Sheep were removed in the early 1900s and replaced by cattle until a court settlement ended livestock ranching in 1998 (McEachern et al., 2009, Anderson et al., 2010). Feral pigs were eliminated by 1993 (Lombardo & Faulkner, 2000). Sport hunting of introduced mule deer (*Odocoileus hemionus*) and elk (*Cervus canadiensis*) was permitted through 2011, after which all non-native ungulates were removed (Morrison et al., 2011; McEachern et al. 2016). Vegetation recovery is likely proceeding at a rate similar to Santa Cruz Island for plant species with wind- or mechanically-dispersed seeds, or small zoochorous seeds (e.g. Wagner et al., 2004, McEachern et al., 2009). In contrast, the recovery of plants with heavy seeds, such as oaks and pines, may be limited by the absence of a long-distance seed disperser on Santa Rosa Island (Pesendorfer et al., 2014).

Model Overview

We developed a spatially-explicit model of island scrub oak population dynamics that consists of two submodels, executed in sequence for each time step: i) a local growth model that describes how oaks age and produce acorns and ii) a dispersal model that describes pre-dispersal predation of acorns and dispersal across the island by gravity or animal-dispersal (Fig. 2; see Appendix A for flowchart and Appendix B for detailed model description). First, we calibrated the model by reconstructing the spread of oak populations on Santa Cruz Island from 1985 to 2005 (Jones et al., 1993; Cohen et al., 2009) using an ensemble ecosystem modelling approach that allowed for the concurrent estimation of predictive parameters (see *Ensemble Model* below; Battogtokh et al., 2002; Baker, Gordon & Bode, 2017). The model considered 500 possible parameter sets, drawn from data-based probability distributions across the respective parameter ranges (Table S1). Model predictions for the spatial and temporal spread of oaks were weighted by each model’s ability (in %) to match the extent of oak habitat recovery that was of observed on Santa Cruz Island between 1985 – 2005. Second, the calibrated model with the weighted parameter settings, excluding pig predation, was applied to Santa Rosa Island to generate a single, weighted-average prediction for the spatial expansion of oak populations over 200 years for each dispersal scenario. A general description of the model components follows; full model details, including a flow chart and parameter ranges are presented as supplementary information (Appendices A & B; Table S1). The model was constructed in MatLab 9.1 (The MathWorks Inc., Natick, MA, 2016). Code, maps, and data used for parameterization are publicly available (Pesendorfer et al., 2017).

Local Growth Submodel

To model oak growth and seed production, we divided the islands into 50 m x 50 m grid cells (100,977 cells on Santa Cruz Island and 86,491 cells on Santa Rosa Island). Each grid cell was populated with trees ranging across 50 age classes from seedlings to mature individuals. Initial demographic composition and growth rate of individual trees comprising each island's simulated population were drawn from measurements of > 1,000 trees on Santa Cruz and > 200 trees on Santa Rosa Island (Pesendorfer et al., 2014). Life history transition probabilities, e.g. from seed to seedling or from seedling to reproductive adult, were derived from acorn germination experiments and a Leslie matrix for island scrub oaks (de Gouvenain & Ansary, 2010; Pesendorfer, 2015). To incorporate density-dependent processes, we also multiplied all growth probabilities by the proportion of unoccupied area in each cell.

Acorn production in *Q. pacifica* varies strongly in space and time, with relatively low spatial synchrony among individuals (Pesendorfer et al., 2014). Acorn production levels were based on 9 years of seed production data on 300 *Q. pacifica* trees, from which values were randomly drawn for each individual cell (Pesendorfer et al., 2014; M. B. Pesendorfer & T. S. Sillett, *unpublished data*). The total number of acorns grown annually by each reproductive-age tree (T_m > 15 – 25 years; de Gouvenain & Ansary, 2010) was derived by multiplying the host cell's assigned seed productivity (acorns/m^2/year) by the tree's crown area (Fig. S1).

Acorn Dispersal Submodel

Acorn predation and dispersal are correlated with local seed production (Vander Wall, 2010; Pesendorfer et al., 2016b). We considered avian and rodent predation of acorns throughout, as well as post-dispersal predation by pigs, which were removed from Santa Cruz Island in 2007, two years after the second vegetation map of the island was created (Cohen et al., 2009; Morrison et al., 2011). The remaining acorns could then move via three dispersal mechanisms: i) scatter-hoarding by island scrub-jays that removed acorns from the tree crown, ii) hoarding of remaining acorns by mice, and iii) random spread, influenced by gravity. Based on published estimates, we assumed that island scrub-jays depredate acorns in any cell, ranging from 40% when acorn production is high to 100% when acorn production is low (DeGange et al., 1989; Pesendorfer et al., 2016b). We then allow island scrub-jays to disperse 50-80% of the remaining acorns (see *Island scrub-jay dispersal* below). Following arboreal removal and caching, we allowed mice to consume the same percentage of acorns as jays, and then disperse 10-90% of the remaining acorns (see *Mouse dispersal*). For Santa Cruz Island only, after all acorns had the opportunity to move, 60-90% were consumed by pigs and removed from the simulation (Suselbeek et al., 2014). Fig. S1 provides model flowcharts for the two contrasting scenarios.

Island scrub-jay dispersal

Individual island scrub-jays scatter-hoard 3,500 to 5,500 acorns a year, with dispersal distances ≤ 400 meters from the parent plant (Pesendorfer et al., 2016b). The birds spatially bias caching of acorns towards areas of high oak seedling recruitment and avoid open or grassy areas (Pesendorfer, Sillett & Morrison, 2017). The birds also transport more than 50% of acorns uphill or across ridges and canyons in ways that cannot be achieved by gravity (Pesendorfer, 2014). On Santa Cruz Island, cells were considered suitable if they contained oaks in 2005. For Santa Rosa Island, suitable cells were determined from a habitat model (Kindsvater 2006), which is based on slope, aspect, and elevation of extant populations of island oaks (*Q. tomentella*), as well as on soil characteristics. This species has narrower habitat specificity than *Q. pacifica*; therefore, this map constitutes a conservative hypothesis of the spatial extent of habitat suitability (Kindsvater, 2006).

Mouse dispersal

Deer mice (*Peromyscus maniculatus*) disperse acorns that have fallen to the ground. In absence of reliable field data from the Channel Islands, we used published values (Thayer & Vander Wall, 2005) to parametrize mouse dispersal of *Q. pacifica* acorns. We allowed the probability that a mouse moves an acorn to vary between 0.1 and 0.9. Because dispersal distances by *Peromyscus* are generally shorter than 10 m, we only allowed acorns to be moved to nearest neighbor cells. We assumed that mice move acorns independently of habitat suitability, because their small home ranges mostly restrict seed movement to short distances.

Gravity dispersal

Acorns not dispersed by an animal vector were allowed to randomly move to a neighboring cell via gravity, depending on a threshold elevation change between two neighboring sites (10 -50 m). The likelihood of passively arriving in a neighboring cell was thus dependent on the slope of the cell. As with rodent dispersal, this procedure was independent of the habitat suitability for scrub oaks in the destination cell.

Ensemble Modelling

We used an ensemble ecosystem modelling approach to predict spatial spread in a situation where system dynamics are highly uncertain. Ensemble ecosystem models use Lotka-Volterra equations to integrate species interaction networks and dynamic community simulations while allowing for parameterization with quantitative and qualitative data for each link between species' populations (Baker et al. 2017). To do so, the model draws random values from each parameter's range and, given the network of interactions, determines potential outcomes. We used these principles to predict spread of the scrub oak. By weighting the parameter set according to the model's ability to re-create a known outcome, the observed expansion of oaks on Santa Cruz Island between 1985 and 2005, we were able to assemble parameter settings that most likely contributed to the observed pattern, given the information about community interactions. This approach provides similar insights to a sensitivity analysis, as the whole range of parameters is explored. Parameter impacts on model outcomes are illustrated by mapping the parameter settings that contributed to the most likely model sets (Fig. S4).

The ensemble model was initiated with the 1985 oak distribution on Santa Cruz Island (Jones et al., 1993). Because the relative oak density for each cell was unknown, starting densities were set at random between 0 and 1. To determine the initial size distribution (age classes) of oaks in each cell, crown diameters were drawn from the distribution over 1,100 trees reported in Pesendorfer et al. (2014). Following each 20-year model run, the predicted oak distribution was compared to the 2005 oak map and the parameter set was weighted accordingly (w_i in Eq. 1; Fig. S2). For example, the weighted average of oak density at position $\boldsymbol{x}$ and time t is given by

$$d(\boldsymbol{x},t) = \frac{\sum_{i=1}^{N} d_i(\boldsymbol{x},t) w_i}{\sum_{j=1}^{N} w_j}, \tag{1}$$

where $d_i(\boldsymbol{x}, t)$ is the density predicted by model i. We calculate uncertainty around model predictions by computing the weighted sample standard deviation.

Results

The gravity-only and mouse-only scenarios produced functionally equivalent outcomes; therefore, we only report the results of the mouse- and jay-dispersal models. The simulation model parameterized with seed dispersal by island scrub-jays and acorn predation by pigs accurately recreated the expansion of oak habitat on Santa Cruz Island in the 20-year period from 1985 to 2005 (Fig. 3; Appendix S2). The best model that included scrub-jay dispersal achieved 92% coverage of the recovery represented by the 2005 vegetation map. In contrast to the best mouse-only dispersal, which achieved 43% of coverage, this jay model captured the strong increase of oak-covered grid cells in the island’s center, particularly in the central valley. In addition, the jay model illustrates how long-distance dispersal allowed oaks to recruit into remote areas without direct connection to existing stands, such as valleys along the island’s north shore (Fig. 3).

Elevational distribution of *Q. pacifica* on Santa Cruz Island was similar under both mouse and jay dispersal scenarios. Maximal recruitment occurred between 100 m to 300 m a.s.l. (Fig. 4). The mean elevation of cells with oak habitat was similar between 1985 (236.4 ± 109.5 m; mean ± 1 S.D.) and 2005 (238.7 ± 110.6 m; *t*-test; $N = 500$, t = 3.36, $P = 0.44$), but the maximum elevation of oak habitat increased slightly, from 638 m to 715 m.

On Santa Rosa Island, the model predicted strong differences in the pace and extent of oak habitat expansion between dispersal scenarios. Oaks would expand slowly in the absence of animal dispersal, benefit somewhat from rodent dispersal (0.7 ha/yr), but fail to expand beyond the general areas occupied in the 1988 habitat map, even over a 200-year period (568.6 ha; Fig 5). Jays dramatically increased the pace of oak expansion (11.2 ha/yr), and expanded the area covered by oaks (2,669 ha; Fig 5). Mean elevation of oak-covered cells would increase from 161.3 ± 67.1 m to 175.7 ± 75.5 m with jay seed dispersal ($N = 500$, $t = 19.61$, $P < 0.001$), but would remain virtually unchanged without jays (162.7 ± 68.5 m; $N = 500$, $t = 1.56$, $P = 0.29$, Fig. 6). The highest elevation of cells with oak cover would increase from 388 m to 465 m. Following the pattern on Santa Cruz Island, the model predicted that jay dispersal would enable colonization of discontinuous regions and new watersheds. Thus, oaks on Santa Rosa Island would spread more rapidly and occupy an area that is four times larger after 200 years than would be predicted in the absence of corvid seed-dispersal (Fig. S5).

Discussion

Recovery Scenarios for Santa Rosa Island

Simulation models of woodland and forest dynamics require an understanding of the seed production and dispersal processes that determine the landscape distribution of tree populations (Aben et al., 2016). We assembled and parametrized a process-based model that captured population dynamics as well as plant-animal interactions of *Q. pacifica*, a keystone species targeted for restoration efforts in the Channel Islands National Park. This model included explicit links between individual-, population-, and landscape-level plant demography, seed production, and their effects on seed dispersers in order to predict oak habitat recovery under three seed dispersal scenarios. Ensemble modelling enabled us to accommodate large knowledge gaps about oak recovery dynamics, incorporate this uncertainty and, using the Santa Cruz Island data for 1985 and 2005, weight parameter sets that accurately represented the system. Our ensemble model provided a rigorous framework to model recovery scenarios for neighboring Santa Rosa Island.

The model results highlight the importance of long-distance seed dispersal by island scrub-jays, as well as the bird's likely role in vegetation recovery since the end of livestock ranching (Sillett et al., 2012; Dahlin et al., 2014). Jay-mediated dispersal of acorns allows new oak stands to establish in suitable areas far beyond the vicinity of existing stands. Such facilitated movement of seeds across fragmented and degraded landscapes is considered one of the key advantages of restoring seed dispersal mutualisms for conservation management (McConkey et al., 2012). Our results, which suggest the pace of oak habitat recovery on Santa Cruz Island required jay scatter-hoarding, also support the hypothesis that removal of > 45,000 sheep starting in the 1980s restored a vital seed dispersal mutualism and enabled it to catalyze oak habitat expansion on Santa Cruz Island (Morrison et al., 2011; Pesendorfer et al., 2017).

Future Scenarios: Caveats & Broader Application

Three assumptions of our model highlight the need for further research. First, the seed predation and dispersal submodel treats dispersal as a mostly homogenous process across spatial scales. Corvid scatter-hoarding of seeds, however, is often context-dependent, so that dispersal rates and distances change with seed abundance and local habitat composition (Pesendorfer et al., 2016b, 2017). Agent-based models are able to integrate such details of animal behavior, but due to the large spatial and temporal scales covered in our study, such an approach would have posed computational challenges (Aben et al., 2016). Second, our model also assumes that a translocated island scrub-jay population would grow as oak populations expand on Santa Rosa Island and provide sufficient acorn dispersal services, as was inferred from Santa Cruz Island (Sillett et al. 2012). A parallel jay population modelling study is underway to test this assumption for Santa Rosa Island. Third, our model assumes that potential oak spread is not limited by soil availability. However, the oak suitability map derived from Kindsvater (2006) does not account for the extensive soil erosion that occurred during the ranching era (see Pinter & Vestal 2005). Further research is needed to understand rates of organic soil development on de-vegetated areas of the California Channel Islands (e.g. Walker et al., 2010).

Despite these caveats, the simulation model underlying the presented scenarios provides a useful tool for assessing the potential for oak population expansion under various seed predation and dispersal scenarios. The spatially-explicit model allows for the comparison of gravity dispersal with other dispersal modes, and can guide the selection and placement of dispersal stepping stones or corridors (Levey et al., 2005; Aben et al., 2016). The model can also incorporate effects of environmental variation by adjusting suitable areas or including changing patterns of seed production, which may exhibit reduced variability with increasing air temperatures (Koenig et al., 2015).

Simulation models have been used to evaluate a variety of conservation strategies (Peterson et al., 2003; Pressey et al., 2007; Bode et al., 2017). For example, in an effort to improve habitat composition for European badgers (*Meles meles*), Van Apeldoorn and colleagues (1998, 2005) developed models that incorporated the animals' demographic and dispersal processes to determine landscape suitability, and informed management actions that significantly increased badger populations. Scenario planning can also include non-biological parameters of management interest – such as budgetary, sociological, and ethical considerations – to help optimize the conservation return on investment (Sarkar et al., 2006). Although our current model focuses on the biological effects of island scrub-jays, it can readily be extended to address other management questions, such as cost effectiveness and broader ecological impacts of different restoration strategies.

To conclude, our simulation model of *Q. pacifica* demographic and seed dispersal processes predicts that recovery of oak populations on Santa Rosa Island would be greatly accelerated by re-establishment of the oak seed dispersal mutualism with island scrub-jays. Rather than focusing on a single target population, our integrated approach considers key interactions between plants and animals (Peterson et al., 2003; Kaiser-Bunbury et al., 2009; McAlpine et al., 2016). To our knowledge, this is the first application of ensemble modelling to determine the impact of species interactions on plant population recovery. We recommend that managers considering large-scale habitat restoration or maintenance projects use realistic planning scenarios that integrate context-dependent ecological interactions. This approach provides the opportunity to investigate a range of strategies targeting multiple species, enabling more rapid and direct recovery of ecosystem function (Samhouri et al., 2017).

Authors' contributions

MBP, CMB, EMM, MB, AKM, SAM, and TSS conceived the ideas; MBP, CMB, AKM, and SAM assembled initial model structure; CMB, MB, and MS implemented the model; MBP and TSS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

The model code, vegetation maps, and data used for parametrization are publicly accessible at figshare doi:10.6084/m9.figshare.5413987.v1 (Pesendorfer et al. 2017).

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Figures

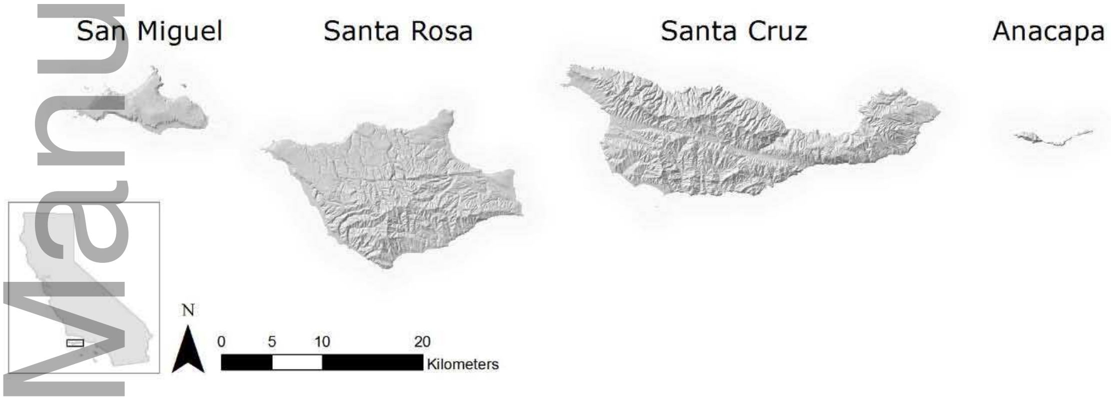


Fig. 1. Santa Cruz and Santa Rosa Islands in the Northern Channel Island Archipelago. The islands are part of the Channel Islands National Park, established in 1980, located in the Southern California Bight (see inset). The park also includes Santa Barbara Island, not depicted here.

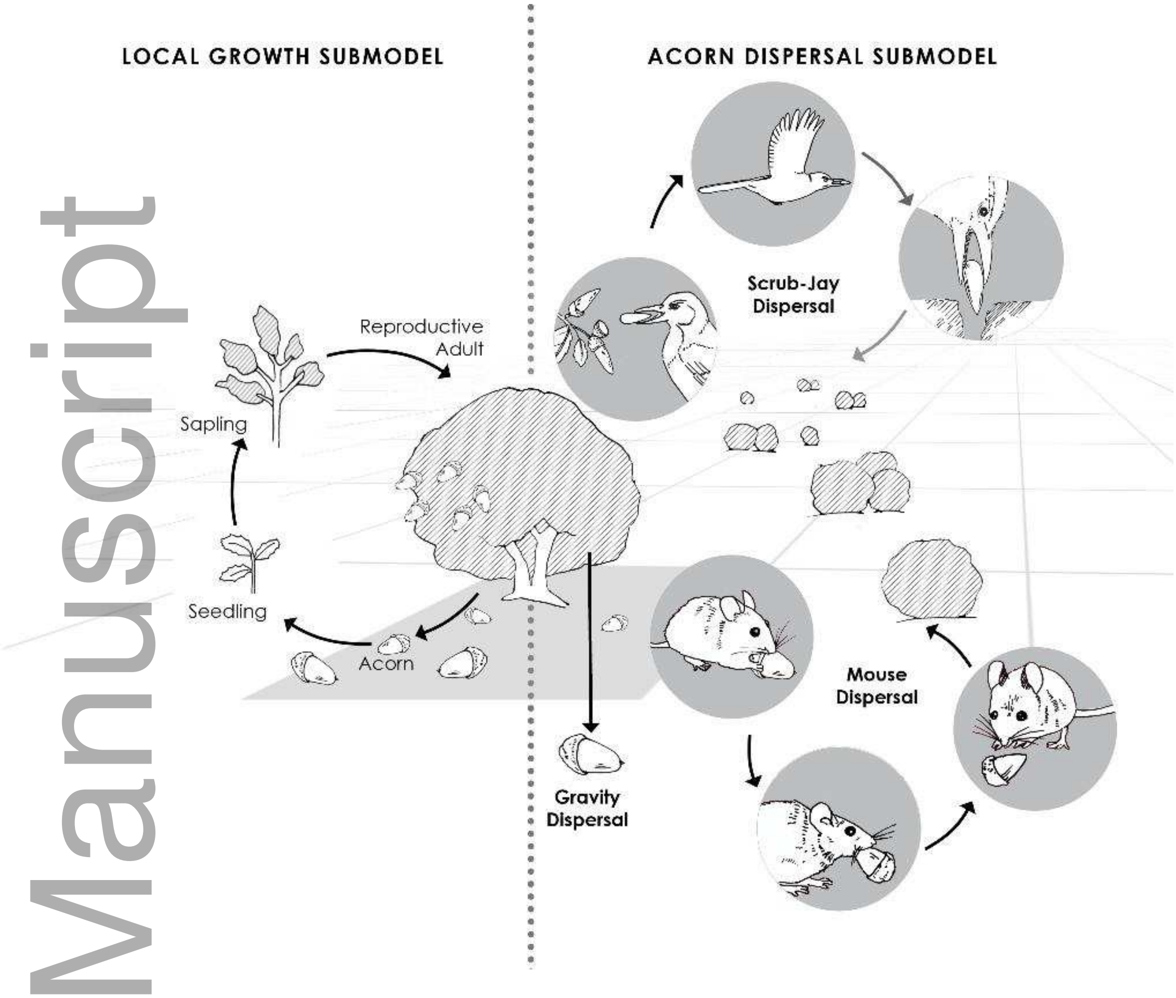


Fig. 2: Visual guide to the simulation model. For each 50 x 50 m square, two sets of processes were modeled. First, the local growth submodel determined growth, mortality, and seed production for all trees. Second, the dispersal model determined the movement and consumption of seeds under different scenarios, by gravity and rodents only, or in the presence of island scrub-jays. All cached seeds that were not recovered or depredated then entered the local growth submodel. (Illustration credit: Emily Underwood).

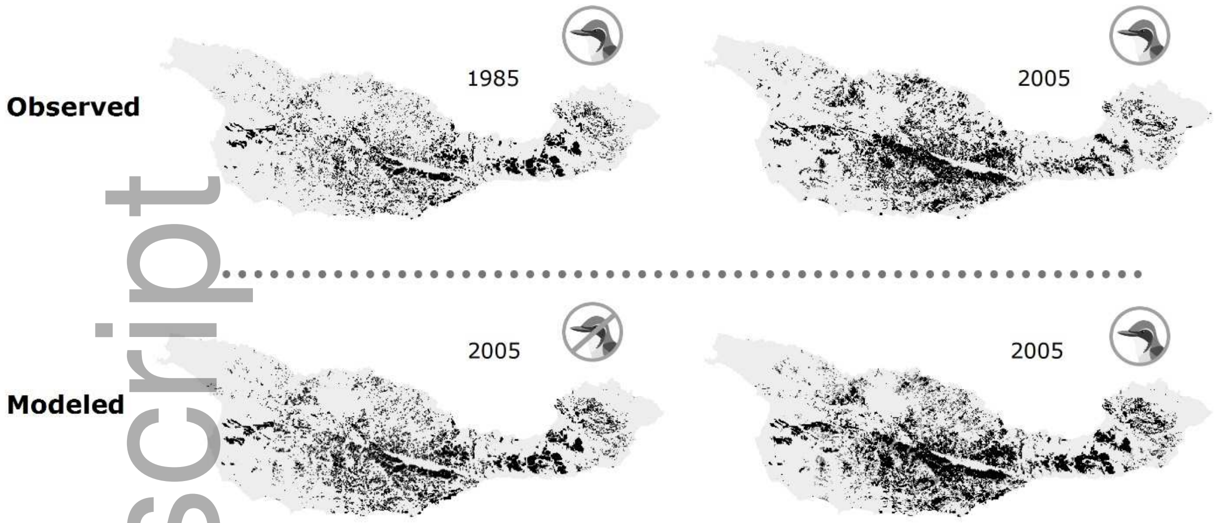


Fig. 3. Model training on Santa Cruz Island. Top: observed oak distribution in 1985 and in 2005, Bottom: simulated 2005 distribution of oak habitat without jay dispersal and in the presence of jays. Black – cells with full oak cover; grey – cells with > 50% oak cover.

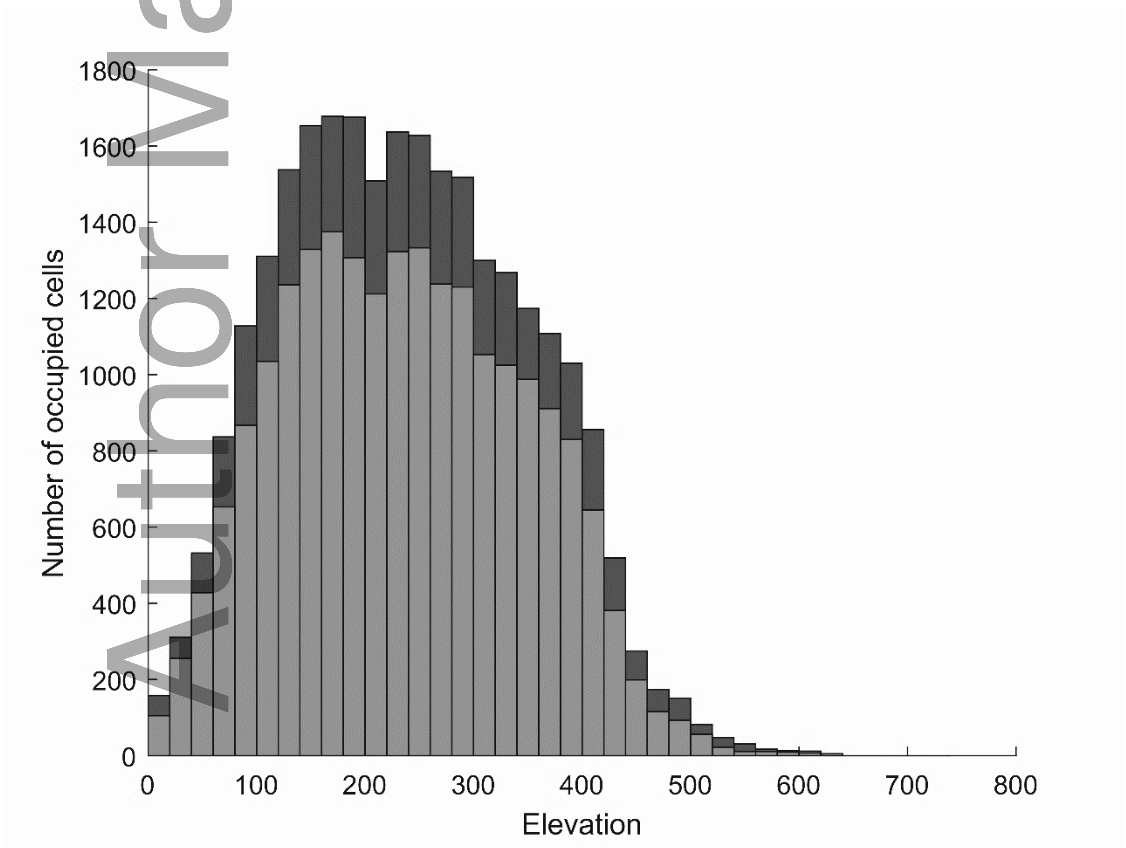


Fig. 4. Historical change in elevational distribution of Santa Cruz Island oak population.

Histogram of 50 x 50 m cells that contain oaks across elevational gradient. Light grey: 1985; dark grey: 2005.

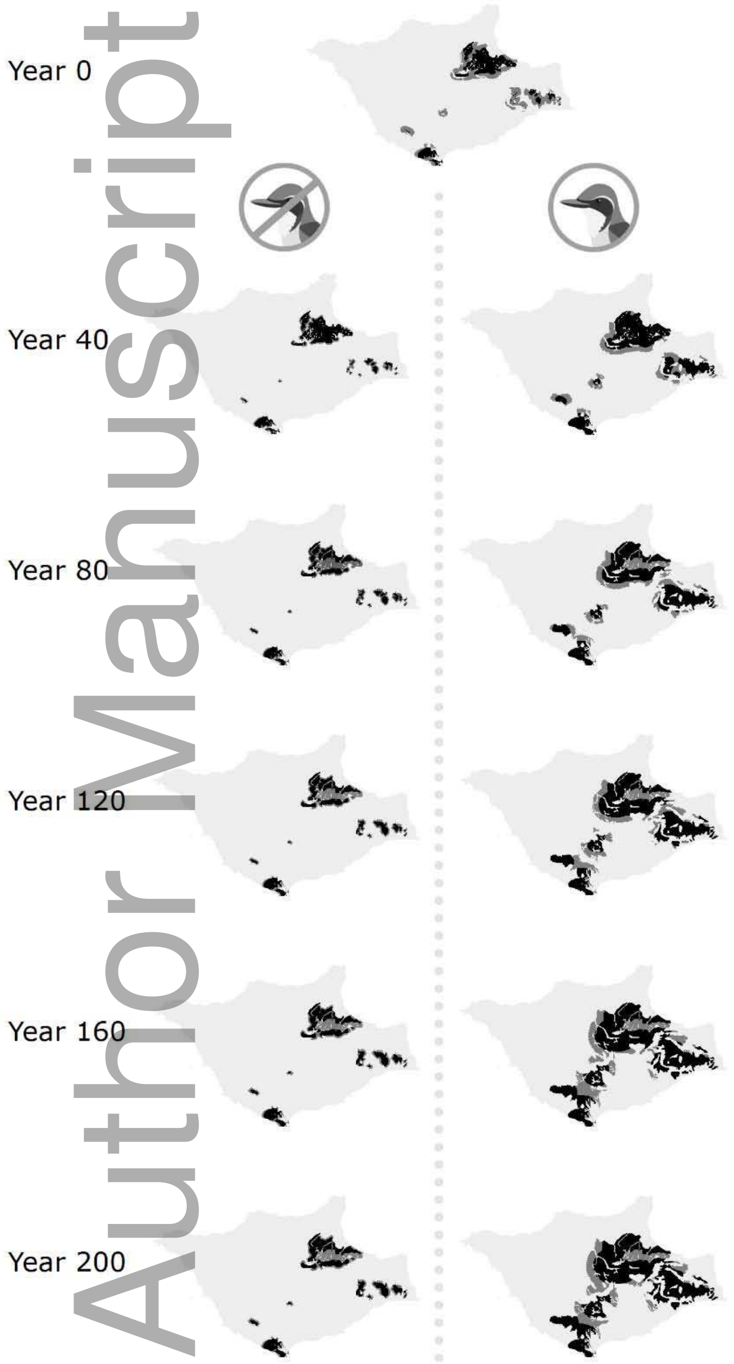


Fig 5. Oak expansion scenarios for Santa Rosa Island. Model-predicted island scrub oak population distribution change over 200 years without and with jay-mediated dispersal. The model was initiated with the 2005 vegetation map. Black – cells with full oak cover; grey – cells with > 50% oak cover.

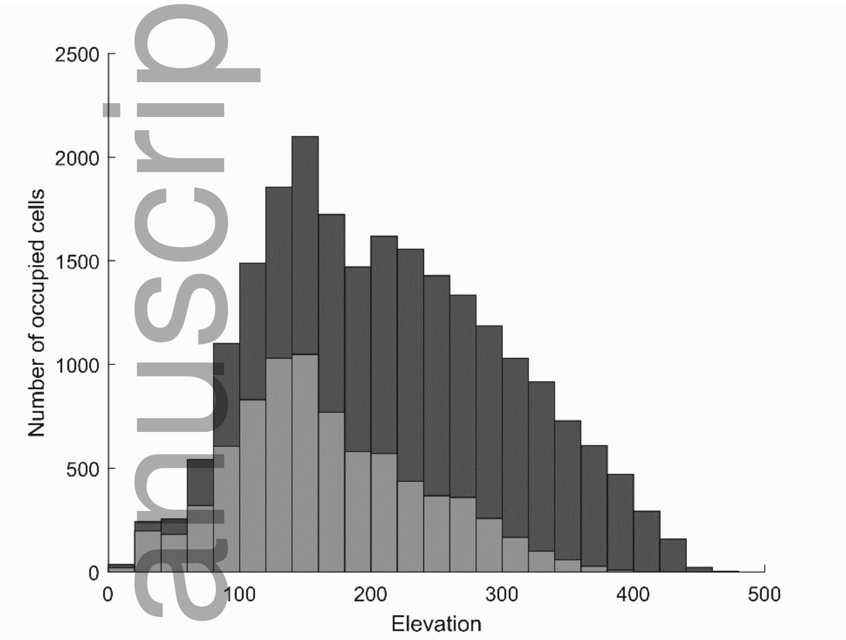
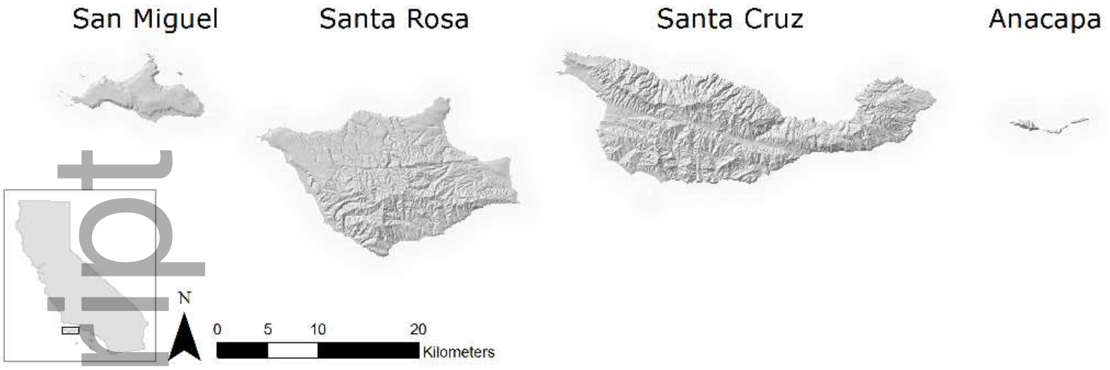


Fig. 6. Model-predicted changes in the elevational distribution of island scrub oaks on Santa Rosa Island. Frequency histogram of 50 x 50 m cells containing oaks. Light grey: 2005; dark grey: predicted distribution after 200 years in the presence of jay-mediated seed dispersal.



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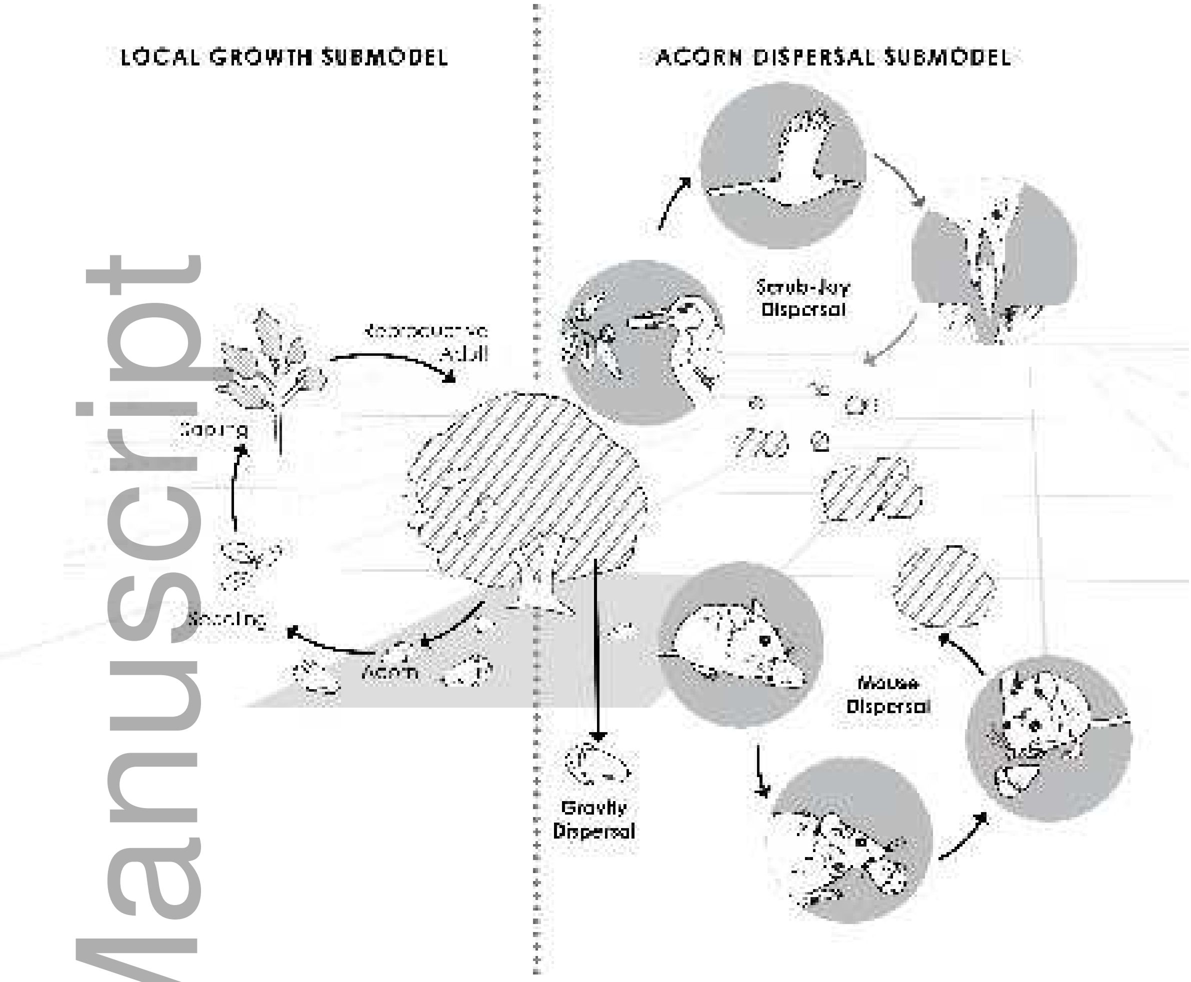

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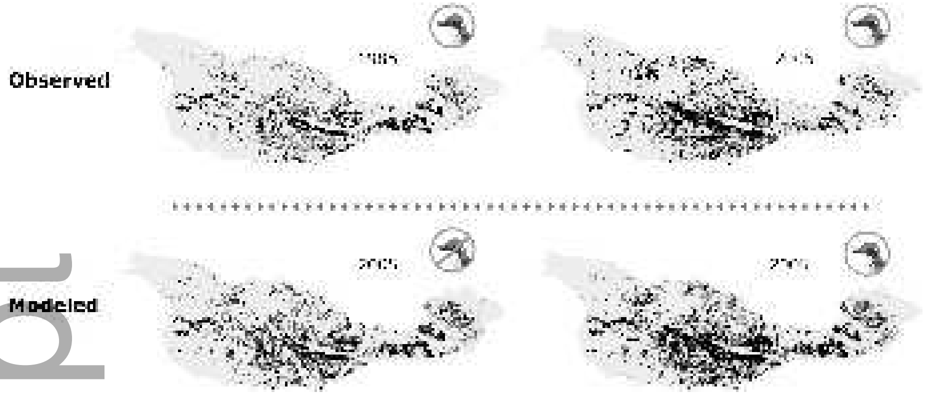

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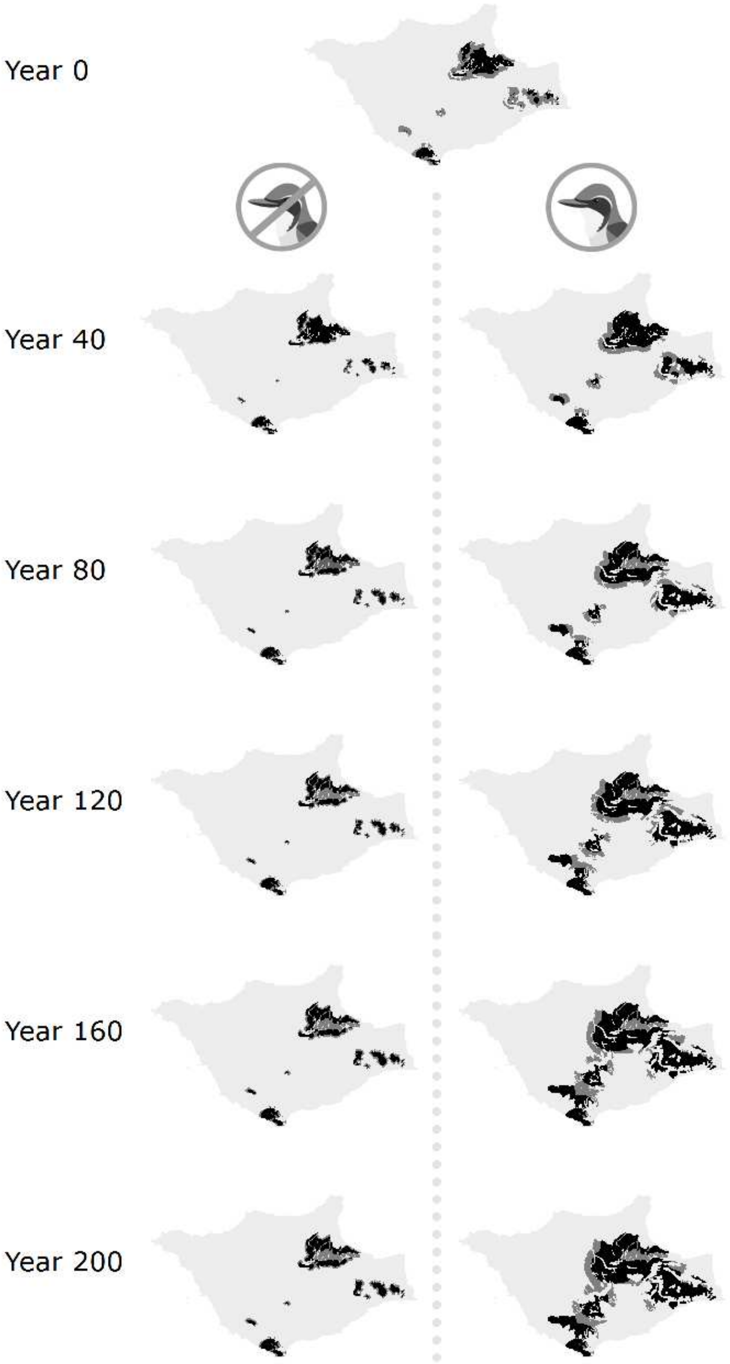

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