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Factors associated with rodent eradication failure

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ABSTRACT

Invasive rodents have an overwhelmingly detrimental impact to native flora and fauna on islands. Rodent eradications from islands have led to valuable biodiversity conservation outcomes. Tropical islands present an additional suite of challenges for rat eradications due to unique characteristics associated with these environments. To date tropical island rat eradications have failed at a higher rate than those undertaken outside the tropics. Critical knowledge gaps exist in our understanding of what drives this outcome. We collated an in-depth dataset of 216 rodenticide based rat eradication operations (33% of all known rodent eradications) in order to determine correlates of eradication failure, including both project implementation factors and target island ecology, geography and climate. We assessed both failed and successful projects, and projects inside and outside the tropics, using random forests, a statistical approach which compensates for high dimensionality within, and correlation among, predictor variables. When assessing all projects, increasing mean annual temperature, particularly above 24 °C, underscored the higher failure rate and greater difficulty of rodent eradications on islands in lower latitudes. We also found clear trends in eradication failure for factors unique to the tropics, including the presence of land crabs – burrowing and hermit crabs, and coconut palms (*Cocos nucifera*). The presence of agriculture was also associated with failure. Aerial operations had a higher success rate than ground-based methods but success with this technique was less likely in the presence of hermit crabs and other non-target bait consumers. Factors associated with failure in ground-based eradication methods suggested limitations to project scaling such as island area and number of staff. Bait station operations were less likely to succeed when using stopping rules based on measures of rodent abundance. Factors influencing rat eradication failure in tropical environments continue to require a deeper understanding of tropical island dynamics to achieve a higher rate of eradication success.

1. Introduction

Invasive rodent species are estimated to have colonized more than 80% of the world's island groups (Atkinson, 1985) where they have been associated with widespread damaging impacts including the extinction or decline of native flora and fauna populations (Campbell and Atkinson, 2002; Jones et al., 2008; Towns et al., 2006) and ecosystem modification (Kurle et al., 2008). Efforts to eradicate invasive rodents from islands have progressed considerably in the past two decades (Howald et al., 2007; Russell et al., 2008; Veitch et al., 2002, 2011), and resulted in demonstrable biodiversity conservation outcomes (Bellingham et al., 2010; Lorvelec and Pascal, 2005). Eradication methods were primarily developed in temperate regions where the majority of rodent eradications have been conducted (Howald et al., 2007). Tropical islands represent an important conservation need given their high biodiversity value (Kricher, 2011; Myers et al., 2000). Tropical island rodent eradications present challenges that contrast with islands in cooler climates, including less temperature aseasonality which provides consistent or rapidly responding food supply to support rodent populations, plus unique biota such as land crabs (Russell and Holmes, 2015; Varnham, 2010; Wegmann et al., 2011). To date the success rate of rat eradications in tropical environments has been lower when compared to non-tropical regions (81 versus 92%, $n = 516$ excluding reinvasions, $\chi^2(1, n = 516) = 11.8$, $p < 0.001$, Russell and Holmes, 2015), and critical knowledge gaps exist in our understanding of what has driven this outcome (Russell and Holmes, 2015; Varnham, 2010). The direct outcome of the higher failure rate in the tropics is that

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populations of those native species identified to benefit from rat eradication remain at risk from invasive species, with indirect implications being a loss of investment – both cost and time to repeat the eradication, biological impacts to native species from the operation, and a potential reduction in confidence in eradication methods.

Central hypotheses for the failure of rodenticide based rodent eradications include inadequate bait availability, low bait palatability, insufficient bait toxicity and toxicant tolerance. These mechanisms represent failed operations whereby rodents survived the operation and repopulated an island and are distinguished from successful operations where rodents subsequently reinvaded and populated an island. Rodent invasion biology and recommendations regarding reinvasion and biosecurity have been reviewed elsewhere (Harris et al., 2012; Russell et al., 2008). Inadequate bait availability implies that some rodents did not have access to sufficient bait due to low application rates, operational deficiencies that resulted in poor bait distribution such as equipment failure, or biological influences such as rodents foraging only in unbaited landscapes (e.g. subterranean features). Low bait palatability suggests that all rodents had access to adequate bait but some individuals did not eat it, or ate an insufficient amount to ingest a lethal dose due to alternative natural or anthropogenic foods that were more desirable or more readily available (Weerakoon and Banks, 2011). Insufficient bait toxicity suggests that all rodents had access to and consumed sufficient bait but not all bait contained a prescribed toxicant concentration for a lethal dose (i.e. bait irregularity) – this is likely a lower risk for eradication projects given there are few bait manufacturers for island eradication purposes and these are subject to rigorous industry standards (e.g. US CFR, 2014). Resistance/tolerance suggests that some rodents accessed and consumed sufficient bait that contained the prescribed concentration of the toxicant but did not die. Resistance is a definition applied to survivors in a population that underwent selection pressure due to chronic exposure to a rodenticide that otherwise would have succumbed to the rodenticide at that dose, and tolerance is typically an *a priori* physiological trait that makes a species less susceptible to a rodenticide – e.g. mice (*Mus* spp.) are more tolerant of anticoagulant rodenticides than rats (MacNicoll, 1993). Resistance has been observed as a genetic adaptation in long-term pest control (Buckle et al., 1994) and should be a lower risk for island eradication projects where prolonged exposure to rodenticides is absent, but is suggested to potentially occur on islands where natural anticoagulants such coumarin occur in plants (Pascal et al., 2008). Bait toxicity and resistance/tolerance are best investigated *a priori* in a laboratory environment. Inadequate bait availability and low bait palatability represent two hypotheses for rodent eradication failure that allow *a posteriori* data collection where relevant operational elements and target island ecology can be investigated.

Determining what causal factors may underlie rodent eradication failure is challenging. As a high cost conservation management intervention there is little scope for experimentally manipulating eradication, c.f. other successful examples of adaptive management in conservation biology (e.g. Whitehead et al., 2008). The number of potential causal factors is also large, multiplicative, and with correlations among them, while the number of rodent eradication failures is comparatively small, potentially making consistent trends hard to detect. Classical statistical analyses of historical efforts can analyse broad trends (e.g. Gregory et al., 2014; MacKay et al., 2007), but will be limited in exploring the breadth or depth of many potential factors. Data-mining methods are suited to such high-dimension data, and have application in diverse fields, especially where users seek to identify important variables from a large pool of candidates (e.g. Cutler and Stevens, 2006; Hochachka et al., 2007). Random forests in particular compensate for correlation among predictor variables (Strobl et al., 2008) and provides a list of predictors ranked by their discriminating power. The identification of variables which have strong correlation with the response then allows the generation of hypotheses of potential causal factors which can be tested in further study, and subsequently used to refine best practice (Keitt et al., 2015).

To date more than 650 eradications of *Rattus rattus*, *Rattus norvegicus* and *Rattus exulans* from more than 527 islands have been attempted globally with outcomes recorded as failed, successful or successful (reinvaded) (DIISE, 2014). When comparing only successful and failed rat eradications using second generation toxicants, aerial operations have a higher success rate (96%, $n = 138$) compared to bait stations (83%, $n = 147$) and hand broadcast (87%, $n = 127$) (DIISE, 2014). While basic information such as target species, method and outcome has been consolidated for each of these projects (DIISE, 2014; Keitt et al., 2011), more detailed operational and environmental data are only available within individual project reports, with varying degrees of detail and availability. Consolidating these data offers an opportunity to quantitatively evaluate rodent eradication operation failures, and particularly what factors are associated with the elevated failure rate in the tropics. We collated data on rat eradication operations, both project implementation factors and target island ecology, geography and climate, in order to determine correlates of eradication success. We used a random forests classification and regression tree (CART) approach (Cutler et al., 2007) which compensates for high dimensionality and correlation among predictor variables (Strobl et al., 2008). This work was motivated by a desire to expand our understanding of the higher failure rate in the tropics by determining the suite of factors that have a consistent relationship with eradication failure throughout the world. We assessed both failed and successful projects, and projects inside and outside the tropics, in order to isolate factors unique to failed tropical *Rattus* eradications.

2. Methods

2.1. Dataset

We used the Database of Islands and Invasive Species Eradications (DIISE, 2014; Keitt et al., 2011) to identify rat eradications undertaken globally. In this database every unique landform from which a rat population was completely and intentionally removed is considered an independent eradication. We selected projects were eradication events were verified either by a primary reference reporting the event, or the event was documented in a peer reviewed summary paper. We excluded islets which we considered functionally part of the principal island on which an eradication took place but do not distinguish 'eradication units' where reinvasion among principal islands in an archipelago is possible (sensu Abdelkrim et al., 2005; Robertson and Gemmell, 2004). We also acknowledge operational dependencies where multiple eradications are conducted under one umbrella of operational planning for logistical efficiency (e.g. shared boat coasts). We selected projects where status could be defined as operational failure (the eradication effort did not eliminate every rodent) or success. We included projects that successfully eliminated every rodent even if the island was subsequently reinvaded but only if reinvasion was robustly confirmed either by genetic analyses (e.g. Russell et al., 2010) or where the time elapsed between the operation and reinvasion excluded operational failure. We selected projects where second generation anti-coagulants (brodifacoum, bromadiolone, difenacoum) were distributed across the entire island during the eradication project and the target species were invasive rats

(*R. exulans*, *R. norvegicus*, *R. rattus*), as these represent rodenticides used in the majority of rodent eradications to date (81% of 516 eradications, DIISE, 2014). We further distinguish aerial from ground-based operations (hand broadcast and bait stations).

We established a set of biological and operational parameters which might influence bait palatability and bait availability and hence the likelihood of eradication success (Supplementary materials). We reviewed peer reviewed and unpublished literature (e.g. operational reports), plus responses from available eradication practitioners with direct experience in these projects, to populate our dataset (available at diise.islandconservation.org). We did not include latitude in our analysis as a predictor and instead included more biologically meaningful climatic proxies which mechanistically describe conditions on tropical and non-tropical islands. We derived four bioclimatic variables from the WorldClim dataset: mean annual temperature, mean temperature seasonality (annual standard deviation of temperature), mean annual precipitation and precipitation seasonality (annual coefficient of variation of precipitation) (Hijmans et al., 2005). WorldClim uses monthly temperature and rainfall values to generate biologically meaningful variables commonly used in ecological modeling (Weigelt et al., 2013), including annual trends and their seasonality. All eradication events were associated with a unique island polygon from the Global Island Dataset (World Conservation Monitoring Center, 2013) approximating island size and location. For each island this set of bioclimatic variables was extracted using zonal statistics (Price et al., 2010) to calculate the mean of variables intersecting with the island polygon using a 1 km buffer where no data overlapped to account for small island size or locational inaccuracies. Where no WorldClim data overlapped with these polygons data were assigned from a nearest neighbor with WorldClim data based on comparable island size. For islands >100 ha neighbors were within 10 km and 100–1000 ha. For islands <100 ha neighbors were within 1 km and <100 ha, or else assigned the average of islands <100 ha with WorldClim data within 100 km ($\sim 1^\circ$ of latitude). Where none of these conditions were met (i.e. no WorldClim data were available for these regions of the globe, such as French Polynesia) we used locally generated meteorological data.

2.2. Analyses

We first tested if our comprehensive database of rat eradications was a random subset of all rat eradications using a logistic generalized linear model with response 'inclusion in our database' compared with the predictor factors of rat species, eradication method, year, eradication outcome, rodenticide, primary method of rodenticide delivery, and our four climate variables (precipitation, precipitation coefficient of variation (CV), temperature and temperature standard deviation (SD). We then analysed the comprehensive dataset using Random Forests (RF), a type of classification and regression tree (CART) machine learning algorithm (Cutler et al., 2007; Prasad et al., 2006). Random forests construct an ensemble of low correlation decision trees on bootstrap subsets of the data, using a random subset of *m* variables for each tree. We implemented conditional trees to account for correlated predictors (Strobl et al., 2008) and to use surrogate splits for missing values in our data (Hapfelmeier et al., 2012). We created 5000 trees each with seven variables. We then estimated the average out-of-bag (OOB) mis-classification error rate for eradication outcome assuming an unacceptable risk of failure where the probability of failure was predicted to be >19% (the current failure rate of tropical eradications). We calculate area-under-the-curve (AUC) unconditional variable importance (Janitza et al., 2013) accounting for missing data (Hapfelmeier et al., 2014). We implement this framework in R 3.0.2 using package party. We interpret our complete set of predictor variables and perform no variable selection (Hapfelmeier and Ulm, 2013). For each analysis variables with importance values greater than the absolute value of the largest negative importance value (i.e. maximum random noise in the data) are considered 'important' (akin to significance) but furthermore we only interpret the most strongly important variables as identified by steps in the variable importance chart. Random forests represent a conceptually different approach to statistical model creation (Breiman, 2001; Hochachka et al., 2007).

We first analyse simultaneously all rat eradication operations regardless of bait distribution method for variables in common across all methods ('general operations'). We then undertake subsidiary analyses for each bait distribution method independently ('aerial broadcast', 'bait station', and 'hand broadcast'), hypothesizing that reasons for eradication failure may be both general to all types of tropical rat eradications or specific to the bait distribution method implemented. Interactive effects were not possible to test due to sample sizes available and the number of parameters tested meaning the number of pair-wise interactions was excessive. In all models we include the fundamental set of climatic covariates: temperature, temperature SD, precipitation, precipitation CV (Russell and Holmes, 2015).

3. Results

We collected comprehensive data for 216 rat eradication operations which represents approximately 56% of 386 available *Rattus* eradications based on our selection criteria, and 33% of all 650 rodent eradications. These eradications were a random subset of all rat eradications by method, date, outcome, primary rodenticide delivery method, precipitation, precipitation CV and temperature. Our subset was not random with respect to rat species (*R. rattus* and *R. norvegicus* under-represented), method used (trapping-toxicant over-represented), and tempSD (low tempSD over-represented). We found no evidence of bias in primary method (aerial, bait or ground) with respect to eradication outcome. For all operations combined we focus only on the top variables above a clear drop in variable importance. For method specific operations we focus on the top four to seven variables all above the threshold for variable importance.

3.1. General operations

Of all 216 events in the dataset, 31 were failures. We identified nine factors that consistently associated with eradication failure (Fig. 1). The mis-classification rate was 17.6%. Eradication failure was most strongly associated with increasing mean annual temperature (particularly for islands >24 °C), increasing island area (particularly for islands >35 km^2), followed by the presence of agriculture. Eradication failure was also associated with high inter-annual variation in precipitation (Precip CV), the presence of coconut trees, burrowing land crabs (Family Gecarcinidae) and the presence of hermit crabs. The primary method used influenced results, with ground-based operations more likely than aerial to fail, and higher staff numbers associated with failure. Among factors not influencing failure rate included whether a secondary eradication method is used, the presence of human habitation, whether any application exclusion was applied (i.e. areas deliberately excluded from bait application such as inland water bodies or sensitive habitat), and whether subterranean refuges might exist.

3.2. Aerial broadcast

A total of 85 aerial broadcast events where 5 failed were analysed. We identified four factors that consistently correlated

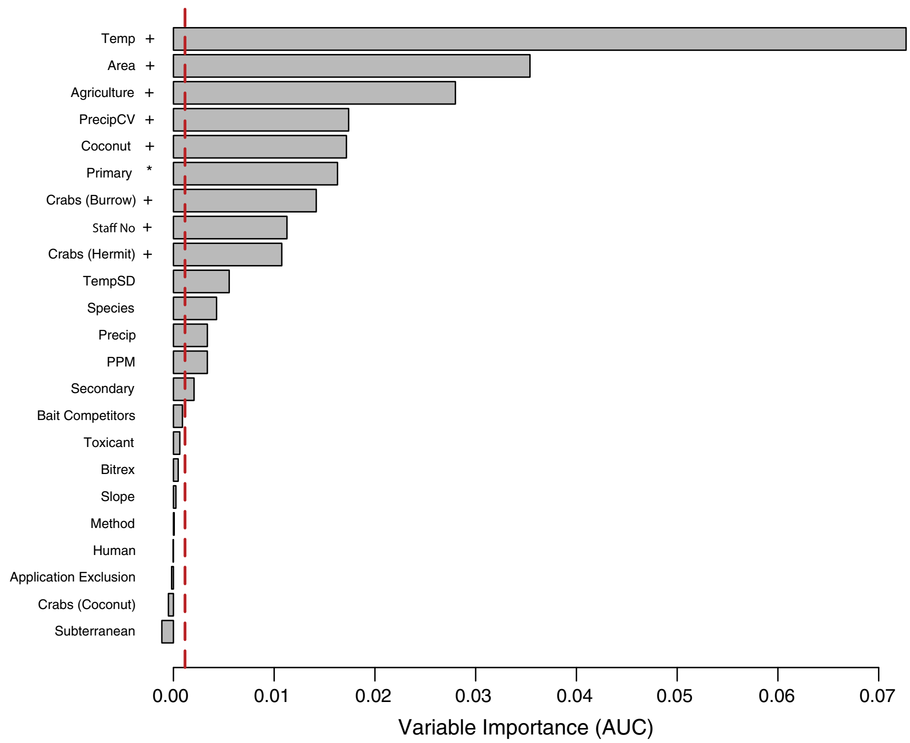

Fig. 1. Variable Importance (calculated by Area Under the Curve) from Conditional Forest analysis of general rat eradication operations. Dashed line indicates variable significance threshold. Signs indicate the direction of the marginal relationship with failure and stars indicate an ordinal or nominal variable that influenced failure rate.

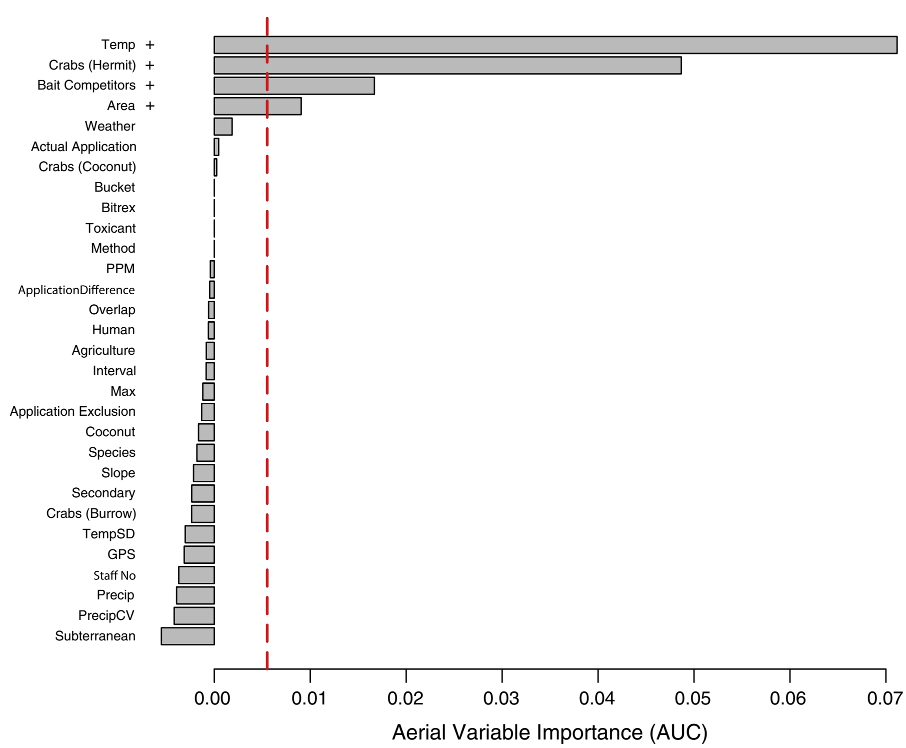

Fig. 2. Variable Importance (calculated by Area Under the Curve) from Conditional Forest analysis of aerial broadcast rat eradication operations. Dashed line indicates variable significance threshold. Signs indicate the direction of the marginal relationship with failure.

with aerial broadcast eradication failure (Fig. 2). The mis-classification rate was 5.8%. Aerial broadcast eradication failure was once again associated with higher annual mean temperatures, as well as the presence of hermit crabs, and other non-target bait consumers (particularly invertebrates, and to a lesser extent birds). Island area was important but less so than when considering all operations combined, or in ground-based operations.

3.3. Hand broadcast

A total of 45 hand broadcast events where 10 failed were analysed. We identified seven factors that consistently correlated with hand broadcast eradication failure (Fig. 3). The mis-classification rate was 55.6%. Hand broadcast eradication failure was most strongly associated with higher precipitation rates, presence of coconut, lower inter-annual variation in annual precipitation. Other factors associated with failure include island area, lower variation in mean annual temperature, total staff numbers and mean annual temperature.

3.4. Bait stations

A total of 86 bait station events where 16 failed were analysed. We identified seven factors which consistently correlated with bait station eradication failure (Fig. 4). The mis-classification rate was 22.1%. Bait station eradication failure was most strongly associated with increasing island size and mean annual temperature. Converse to hand broadcast, higher variation in inter-annual precipitation was associated with failure. Other factors associated with failure included the presence of burrowing land crabs, higher staff numbers, the presence of agriculture and the use of a stopping rule based on measures of rodent abundance.

4. Discussion

Invasive alien mammal eradication is an important tool to protect native biodiversity (Bellingham et al., 2010; Lavers et al., 2010; Lorvelec and Pascal, 2005). While we explored factors associated with *Rattus* eradication failure, we note that the overall success rate remains admirably high for a conservation intervention (87%, $n = 516$). It is realistic to expect that the unique circumstances of individual islands, and the stochasticity of natural systems, will inevitably lead to some eradication failures. In particular, the small number of aerial eradications which have failed makes it difficult to determine systemic factors which may contribute to these failures but a number of key correlations were nonetheless identified. While these will offer setbacks for individual projects, eradication failures, when adequately reviewed and documented offer the broader conservation community the opportunity to learn and develop new techniques to protect island native biodiversity (e.g. Russell et al., 2015). Our retrospective data collection excluded some direct and detailed parameters that may influence the likelihood of project failure, such as cumulative rainfall leading up to an operation (Pott et al., 2015), vegetation types and diversity (US Fish and Wildlife Service, 2011), or assessment of the presence of rodent breeding. In our study we were also unable to assess interactions between predictors which may affect eradication outcome and for some operations this may have been be an important contribution of failure. Other study approaches that can help shed light on factors influencing failure amongst tropical projects include assessment of successful eradications on islands where previous efforts have failed, and more in-depth reviews of successful and failed projects where more detailed information is available (Varnham, 2010). We also consider this study distinct from investigations into new and 'game-changing' technologies that will allow invasive species to be eradicated with greater efficacy (Campbell et al., 2015; Saunders et al., 2010). However, while these innovations are critical in creating tools for future eradications they are unlikely to be available in the near future (Campbell et al., 2015). Our results provide the greatest utility for informing *Rattus* spp. eradications on islands using second generation anticoagulants but we expect the results to generally inform eradications on other similar species (e.g. *Mus* spp.) and with comparable operational strategies involved, including first generation anticoagulants, or eradications within predator proof fences (Young et al., 2013). This study, and other *a posteriori*

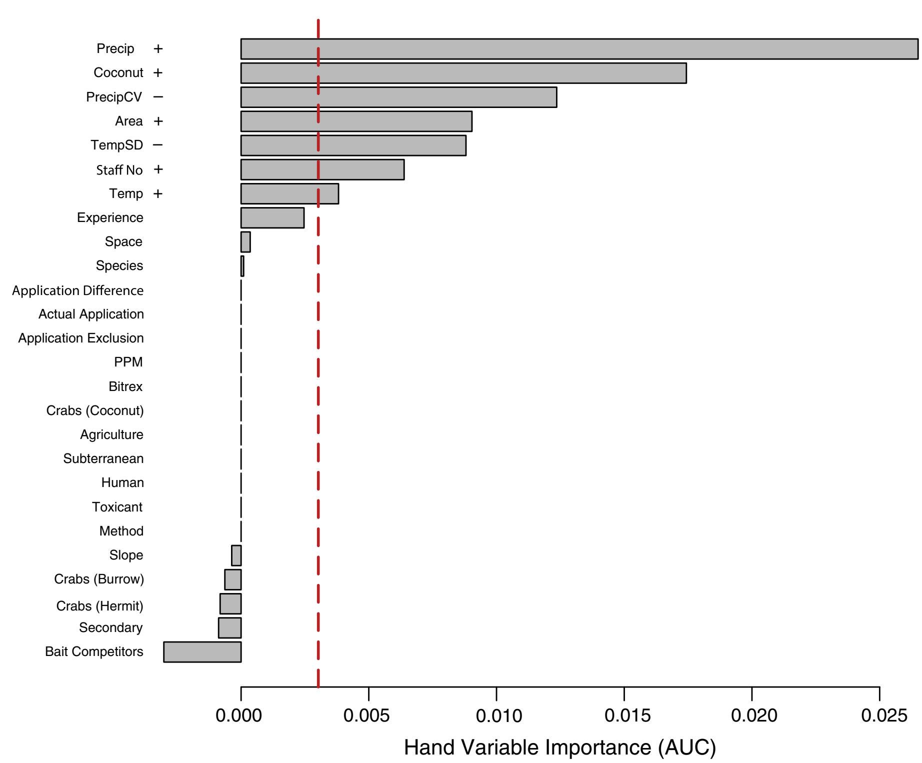

Fig. 3. Variable Importance (calculated by Area Under the Curve) from Conditional Forest analysis of hand broadcast rat eradication operations. Dashed line indicates variable significance threshold. Signs indicate the direction of the marginal relationship with failure.

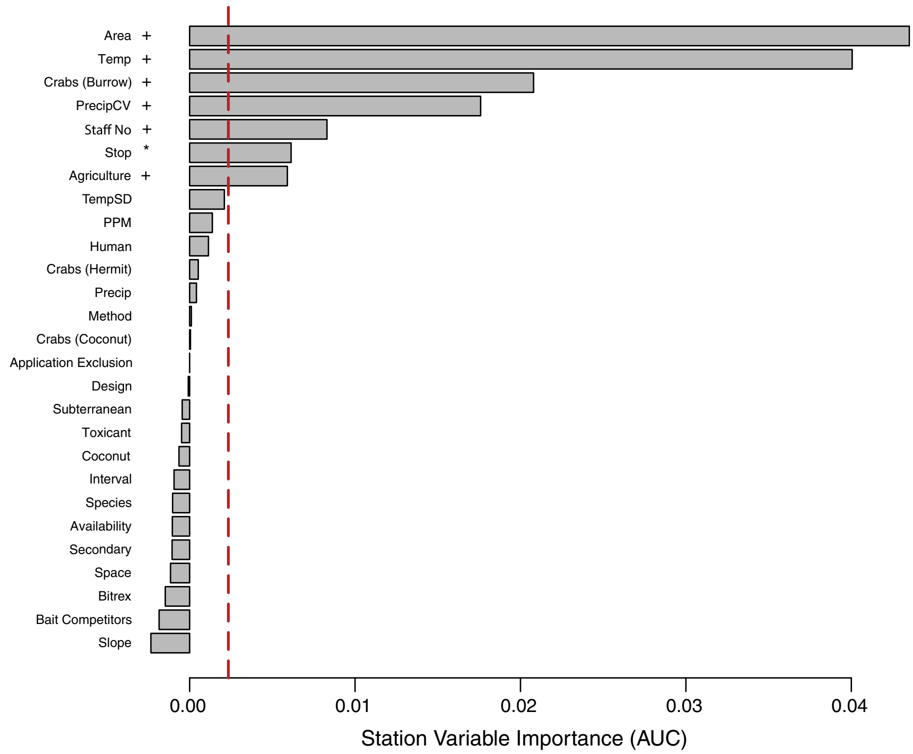

Fig. 4. Variable Importance (calculated by Area Under the Curve) from Conditional Forest analysis of bait station rat eradication operations. Dashed line indicates variable significance threshold. Signs indicate the direction of the marginal relationship with failure and stars indicate an ordinal or nominal variable that influenced failure rate.

investigations, (Gregory et al., 2014; MacKay et al., 2007) have additional utility for suggesting the most important data to collect to inform post-eradication review (Keitt et al., 2015).

Increasing mean annual temperature underscored a higher failure rate and greater challenge of rodent eradications on islands in lower latitudes, with projects on islands with a mean annual temperature above 24 °C having a higher failure rate. Higher temperatures are more likely to facilitate environmental outcomes of reduced bait availability (by providing a more consistent food supply that allows breeding, and isolates female rodents and young) and bait palatability (by providing alternative natural food supply). When all operations were considered, islands with high intra-yearly variation in precipitation were more likely to fail. When assessing individual methods this trend was observed when using bait stations whereas the opposite trend was observed amongst hand broadcast, confounding interpretation of this result. While this outcome may be an artifact of the projects sampled, it does suggests that failure is possible across a range of precipitation CV values making this climatic variable less reliable as a general predictor of eradication failure, and suggesting there is a more complex relationship of precipitation CV and project outcome. Tropical regions are characterized by higher temperatures with little year round variation, and many yielding some of the highest annual precipitation rates recorded globally (Holdridge, 1947; Kricher, 2011). Precipitation on tropical islands can vary little over the course of a year (e.g. Palmyra Atoll), or show pronounced seasonality between wet and dry periods (e.g. Isabel Island) (Russell and Holmes, 2015). These climatic conditions drive primary productivity on islands (Kricher, 2011) that ultimately regulate invasive rodent populations by providing more consistent food supply throughout the year which in turn facilitates breeding, or allows populations to resume breeding rapidly when rainfall occurs (Russell et al., 2011; Russell and Ruffino, 2012). Thus it may be more difficult to time an eradication on tropical islands either because there is not a well-defined period of less productivity, or because rodent populations could respond to unpredictable aseasonal events. In contrast, islands in cooler temperate climates have pronounced seasonality in temperature that cause a predictable annual decline in productivity, rodent breeding and concomitant declines in invasive rodent populations, which can then be targeted for eradication. Optimal timing for tropical island rodent eradications in different seasonal precipitation gradients is an important avenue for further investigation.

Consistent with other reports we also found clear trends with eradication failure for factors unique to the tropics known to confound rodent eradications, including the presence of burrowing land crabs and hermit crabs, and coconut trees (Varnham, 2010; Wegmann et al., 2011). While each of these factors are common in the tropics they are not necessarily ubiquitous (e.g. these are all absent in the Galapagos Islands), suggesting each of these will be important to consider when planning individual tropical eradications. We only found limited evidence of a higher failure rate when *R. exulans* was targeted, probably due to the range of *R. exulans* being primarily limited to the tropical Pacific (New Zealand is an exception), which suggests the underlying factors driving a higher failure rate in warmer locations are ecologically relevant to all three species. While we found no evidence for trends amongst many other factors assessed, such as areas excluded from bait application by a particular method and the presence of human habitation, we still consider these to be potential risk factors for projects on a case by case basis.

Non-target bait consumers can increase risk of eradication failure by reducing bait availability for rodents (Griffiths et al., 2011). For tropical island eradications, land crabs have previously been highlighted as a likely contributing cause in other failed projects (Wegmann et al., 2011), and we found a similar result with hermit crabs *Coenobita* spp. and burrowing land crabs (Family Gecarcinidae) primarily for aerial and bait station operations. These species have been demonstrated to consume bait and prevent access to bait either through swamping behavior, blocking access to bait stations (hermit crabs) or caching bait (burrowing land crabs) (Wegmann, 2008), and can consume anticoagulant rodenticides with minimal physiological impact (Pain et al., 2000). The aseasonality of land crab reproduction and increased activity during wet periods (Buggren and McMahon, 1988), plus their ability to consume significant amounts of bait and interfere with traps and detection devices, make it challenging to plan the timing of eradication operations in their presence (Wegmann, 2008). More recent mitigation techniques for bait station projects have modified station design or placement (Hayes et al., 2004; Witmer et al., 2007). In the case of broadcast projects, the bait consumption rates by crabs were explicitly calculated (e.g. Cuthbert et al., 2012), and used to inform bait application rates that account for the quantities consumed by land crabs and ensure sufficient bait availability for rodents while avoiding as much as possible harm to non-target species (US Fish and Wildlife Service, 2011). Development of a crab deterrent compound for bait matrices offers a potential innovation to reduce land crab consumption in future tropical rodent eradications (Campbell et al., 2015), and should be further investigated. We also found evidence of non-target bait consumers other than land crabs possibly influencing failure rate. Identifying the role of these potential non-target bait consumers in a simple food web can aid understanding of how these animals may interact with bait. Birds and invertebrates will likely be island specific non-target bait consumers and for invertebrates will be influenced by seasonal phenology, and for birds by learning behavior.

We also found combined evidence for higher likelihood of failure on islands where coconut palm *Cocos nucifera* or agriculture was present. Both may increase eradication risk by reducing bait palatability by providing alternative food supply, and the coconut palm may also reduce bait availability by providing an alternative substrate that rodents can occupy. The coconut palm is common on tropical islands globally (Harries, 1978). Coconut fruit is a potential food alternative for rodents (Russell et al., 2015), and the canopy of coconut palms provide rats (particularly *R. exulans* and *R. rattus*) an arboreal habitat for nesting and feeding which can limit access to bait when distributed solely on the ground (Wegmann et al., 2011). The presence of agriculture was also consistently important, and although not unique to the tropics, the types of crops and their productivity in tropical environments have long been a focus for research in rodent control and management (Oerke, 2006), as they may provide alternative food for rodent populations during baiting operations and support rodent breeding. Integrating lessons learned from agricultural based research on rodents may offer important insight for rodent eradications.

Other factors strongly associated with failure can be interpreted as potential limits on the ability to scale eradications (e.g. area or number of staff), and likely reflect operational challenges in achieving adequate bait availability. This outcome was primarily influenced by method, suggesting the challenges to successful rat eradication depend on the method used. Aerial broadcast projects have the highest success rate, and area was less of a limiting factor compared to the presence of hermit crabs and other non-target bait consumers. Ground-based eradication projects assessed appeared more limited by factors associated with project scaling. For ground based operations, higher numbers of staff are required to bait larger islands, and failure to achieve satisfactory bait coverage by any one individual can put a project at risk. This contrasts with most aerial projects where the pilots have sole responsibility for bait distribution. Bait station operations where stopping rules were based on measures of rodent abundance were also associated with failure possibly reflecting the challenges of detecting rodents at low densities (Russell et al., 2005). Ensuring adequate sampling for rodents during bait station operations is paramount for determining when to stop or continue baiting. The parameters used in our model had poor ability to predict success or failure for hand broadcast method and we offer caution planning an eradication using this method, as the factors influencing outcome are less clear. Howald et al., (2007) suggest that rodent eradications on islands <100 ha should be considered routine. The 95th percentile for successful projects in the tropical latitudes using hand broadcast methods is 47 ha ($n = 74$), and 164 ha for bait station ($n = 84$) (DIISE, 2014), suggesting about 50 and 200 ha respectively may represent precautionary size limitations for these eradications methods in tropical environments. Above these island areas, aerial broadcast should be considered, and guided by recommendations for best-practice and other key principles for rodent eradication (Broome et al., 2014; Cromarty et al., 2002).

The factors associated with rat eradication failure in general, and particularly in tropical environments, appear to be many and potentially multiplicative. The holistic complexity of eradications will always be a challenge regardless of environment, and requires eradication implementation following best practice (Broome et al., 2014). Factors unique to tropical island ecosystems clearly play a role in the increased eradication failure rate observed in the tropics, requiring their own set of recommendations for best practice (Keitt et al., 2015). Concurrently, operational aspects of rat eradications, including those specific to bait application method, will also impact the outcome and require careful consideration when applied to particular islands. We have presented factors and recommendations which we believe eradication practitioners should consider as influencing the outcome of rat eradication operations. In the future, biologists will need to further contribute to our understanding of tropical island dynamics, particularly with respect to eradication, while eradication practitioners should seek to understand more deeply the role of tropical environments in eradication success. This includes factors such as; rodent foraging behavior amongst more abundant food supply (Ringler et al., 2014); the role and behavior of major non-target bait consumers such as crabs (Wegmann, 2008); interspecific interactions between rodents and non-target bait consumers (Russell et al., 2015); and the behavior of rodents actively breeding during an eradication effort (Harper et al., 2015). Future research should be targeted to address knowledge gaps in both bait availability and palatability including rodent diet and population ecology, toxicant delivery and formulation, improving operational implementation, and non-target bait consumers (Keitt et al., 2015).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.12.018.

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