REVELATIONS ON SERPENTS AND DEVILS: PREDICTIVE ROADKILL RISK MODELS IN ISLAND SYSTEMS INFORMED BY CITIZEN SCIENCE

A Dissertation

by

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ABSTRACT

Habitat change is widely considered the primary cause of biodiversity loss and the expansion of infrastructure, especially roads, will bring ecological consequences to biodiversity. Consequences of roads on biodiversity include habitat loss, fragmentation, and among the most insidious causes of impoverishment of vertebrate populations, roadkill. My dissertation focused on understanding the magnitude of roadkill and developed novel predictive roadkill risk modeling as a conservation tool in two island systems.

We conducted the first synthesis of data from a large citizen science program, the Taiwan Roadkill Observation Network (TaiRON), and quantified the magnitude of roadkill in Taiwan to understand which taxa were of greatest conservation need. Notably, the study revealed that snakes were the largest proportion of all roadkill (35%) and 26% of snake roadkills were of protected species. Additionally, the top 23 species of a total 496 species ranked by roadkill abundance made up 50% of the observations. Importantly, certain taxonomic groups were disproportionately killed on roads, and a small number of species account for most of the mortality.

We analyzed TaiRON roadkill observations in a novel use of the SDM, MaxEnt, to predict relative roadkill risk across the Taiwan road network and to identify high roadkill risk areas for the taxa with conservation need. Our analyses highlighted key environmental variables that impacted roadkill risk for different guilds and species modeled. The roadkill prediction models performed well across ecological levels on a

national scale. This study demonstrated that the predictive roadkill models are ecologically and geographically scalable to address ecological questions of interest.

Finally, we developed a predictive relative roadkill risk model for the Tasmanian devil (*Sarcophilus harrisii*). I compared the applicability of the roadkill risk modeling methodology in a contrasting landscape to expose challenges in other systems. Relative to Taiwan, Tasmania is sparsely populated by humans, has a low road density, and has a less established roadkill monitoring program. Nevertheless, high model performance in predicting roadkill risk in a contrasting system suggests global applicability of the methodology, even when roadkill data is less abundant than from databases of larger programs.

DEDICATION

The undertaking of my dissertation would not be possible without the great love and support of my mother, Sarah S. Chen, and this work is dedicated in part to her. I also dedicate this work to all the Asian-American girls who have not been supported in their curiosity for and love of ecological and field sciences. You are not alone in your “non-traditional” interests, and you don’t have to be *that* kind of doctor ☺

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1. INTRODUCTION

1.1. Introduction

Encountering wildlife on roads can be a shocking everyday reminder of the hazards of roads. These encounters between humans and wildlife on roads are a common occurrence, and for many, a primary source of interaction with wildlife. Unfortunately, this literal intersection of humans and wildlife often has major consequences. Roads can be detrimental to humans when interactions between drivers and wildlife collide, and these wildlife-vehicle collisions (WVCs) cost US society over an estimated 8 billion dollars per year (Huijser, McGowen, Fuller, Hardy, & Kociolek, 2007). There are also many major ecological consequences of roads as they are one of the greatest threats to wildlife on Earth (Trombulak & Frissell, 2000).

Road networks require the removal of wildlife habitat, so in existing, a road is environmentally and ecologically impactful. They can create direct ecological impacts such as impacts during removal of habitat and construction of the road and road kill, or indirect ecological impacts such as pollution runoff or act as a genetic barrier (Andrews, Gibbons, & Jochimsen, 2006; Coffin, 2007; Forman & Alexander, 1998; Holderegger & Di Giulio, 2010). Roads are a major cause of fragmentation for wildlife (Leavitt & Fitzgerald, 2013; van der Ree, Jaeger, van der Grift, & Clevenger, 2011; Walkup, Leavitt, & Fitzgerald, 2017), and they often trigger 'contagious' development, where roads "provide access to previously remote areas, thus opening them up for even more roads, triggering land-use changes, resource extraction, and human disturbance" (Selva, Switalski, Kreft, & Ibisch, 2015). The study of these ecological impacts is termed road ecology, and it is a relatively new academic field, but its traditions are old.

Among one of the first few road ecologists was the prominent ecological figure, Joseph Grinnell. As an avid naturalist, he kept logs of road-killed wildlife that he would later publish. The road ecology literature of the early 1900s, when roads were less ubiquitous and driving was reserved for those who could afford it, was mostly lists of dead wildlife (Kroll, 2015). The next major advance for the study of road ecology was post-WWII, when road building and car ownership boomed. In the 1980s, the literature began to include ecological considerations in highways, mainly spurred on by the many roadkill cases of the endangered Florida panther (Maehr, 1989) and because collisions with deer became an increasingly dangerous problem. Finally, in 1996, the first seminar on road ecology was held where Dr. Richard Forman coined the term for the growing discipline (Kroll 2015).

For the remainder of the 1990s through early 2000s, road ecology was mainly a descriptive discipline (Coffin, 2007; Forman et al., 2003). In 2000, Forman again termed the “road-effect zone” as the area of ecological effects created by a road, and spatial ecology was incorporated into literature (Forman, 2000). Much of the literature was still focused on mitigation of the extensive road networks built throughout the 1950s-1990s, such as eco-passages and corridors, and was mainly evaluative of mitigation in single localities or single stretches of highways rather than landscape scale approaches (van der Ree, Smith, & Grilo, 2015). The other main branch of road ecology quantified ecological impacts of roads in terms of landscape ecological concepts such as fragmentation and edge-effects (Andrews et al., 2006; Eigenbrod, Hecnar, & Fahrig, 2009; Glista, DeVault, & DeWoody, 2008; Jaeger, Fahrig, & Ewald, 2005; Munro, Bowman, & Fahrig, 2013; Rytwinski & Fahrig, 2007). During this period, many of the questions in road ecology research were still focused on explaining the effects of roads rather than predicting them (Fahrig & Rytwinski, 2009).

In the mid-2000s, road ecology made the jump from descriptive to predictive and predictive studies became a budding branch of road ecology (Gunson, Mountrakis, & Quackenbush, 2011). Researchers started incorporating linear regressions and general linear models to predict possible areas of mitigation (Clevenger, Chruszcz, & Gunson, 2003; Malo, Suárez, & Diez, 2004) during this time. As spatial tools and data became more advanced, researchers began utilizing these new spatial tools to detect non-random spatial clusters of road kill data, or road kill "hotspots," a descriptive analysis, such as with the ArcGIS Getis-Ord* hotspot analysis (Shilling & Waetjen, 2012). Road ecologists were enabled to explore more environmentally relevant questions that were both descriptive as well as predictive.

Many road ecologists are still working on local mitigation studies of direct impacts of current roads, be it through eco-passages, fencing, infrared wildlife detection systems, advanced cameras, pressure sensing roads, or other developments in technology that have continually expanded mitigation options (Huijser, Mosler-Berger, Olsson, & Strein, 2015; Lester, 2015; Smith, Van Der Ree, & Rosell, 2015; van der Ree, Gagnon, & Smith, 2015). This applied facet of road ecology will continue to have importance in the discipline as it is the interface at which other road ecology research is tested for effectiveness. However, research in road ecology has steadily moved away from the study of impacts on single stretches of roads or highways and has widened its scope to broader landscape scale processes as there is a need to document higher order effects of roads (van der Ree, Smith, et al., 2015). Hotspot analyses are a popular tool for larger-scale roadkill analyses, but there have been findings that hotspot analyses may not be useful indicators for road mitigation measures on older roads that have already depressed populations of wildlife, but could be helpful for newer roads (Eberhardt, Mitchell, & Fahrig, 2013; Zimmermann Teixeira et al., 2017). This was an important finding as it directly translates to conservation and mitigation actions on the ground and suggests utilizing other methods for identifying areas in need of roadkill mitigation, especially for established road networks.

For this and the following reasons, my research focuses on using species distribution models (SDMs) to create predictive roadkill maps, rather than hotspot analyses. Predictive SDM roadkill models have the advantage of predicting both relative roadkill risk outside of areas we have roadkill data and can identify the variables that best explain presence of roadkill, whereas hotspot and cluster analyses can only highlight spatially clustered data and cannot predict into unsampled areas as they do not incorporate environmental or landscape variables. Previous studies have used various predictive models for analysis on roadkill (Gomes, Grilo, Silva, & Mira, 2008; Malo et al., 2004; Ramp, Caldwell, Edwards, Warton, & Croft, 2005), but few studies have employed MaxEnt for vertebrate road mortality (Garrote, López, López, Ruiz, & Simón, 2018; Ha & Shilling, 2017; Kantola, Tracy, Baum, Quinn, & Coulson, 2019; Lin et al., 2019). My research provides novel use of MaxEnt to predict roadkill mortality across a road network utilizing a large and robust citizen science database.

Big data and global scope have recently entered the realm of road ecology, and road ecologists' foray into big data is usually through citizen science. As roadkill is a prominent avenue of public interaction with wildlife, several projects have harnessed the human capital of citizens affected and concerned by wildlife road mortality. The first was the California Road Observation System (CROS), which was started by Fraser Shilling in 2009. Since then, dozens of roadkill observation systems have cropped up all over the world, including those focused on singular endangered species (e.g. the Save the Tasmanian Devil Program (STDP)), and others that are encompassing of any wildlife found, one of the most extensive being the Taiwan Road Observation Network (TaiRON). Through roadkill databases, citizen scientists equipped with a GPS and camera-enabled smartphone have an opportunity to engage with conservation and are an invaluable source of data for roadkill studies in the future. With increasing ability to monitor effects of roads through citizen science networks, sensing technologies, and overall increase in availability of environmental data, predictive roadkill risk modeling is also gaining credibility. As predictive roadkill risk models have the power to test a priori hypotheses and project mitigation options for testing, they are powerful tools in road ecology.

In my international research, I incorporate both large crowd sourced datasets and predictive modeling methods to develop ecologically attuned tools for applied conservation in road ecology. I quantified patterns of roadkill and elucidated wildlife groups that are most heavily impacted in Taiwan. Additionally, I aimed to develop a novel use of a modeling methodology to predict relative roadkill risk across a road network for species and guilds of conservation concern in Taiwan and Australia. I tested this model across scales, both ecologically (from species to guilds) and spatially (in two contrasting systems).

As a student in the Texas A&M University Applied Biodiversity Science Program (ABS), I built a network of global collaborations, and have conducted studies as the principle investigator in Taiwan as a fellow with the National Science Foundation's (NSF) East Asia and Pacific Summer Institute (EAPSI) during Summer 2015, a Fulbright Research Fellow in Taiwan during 2016- 2017, and an Endeavour Research Fellow in Australia in 2018. In accordance to ABS tenets, my project extended scientific involvement to local Taiwanese and Australian actors and institutions in conservation of their unique wildlife through participation, and has fostered international collaboration between American, Taiwanese, and Australian researchers and institutions. The outcomes of my research have produced interactive predictive roadkill tools for collaborators and will continue to be fruitful for wildlife conservation globally.

In Chapter 2, I highlight the magnitude and importance of large, national, citizen science roadkill observation programs. I describe the patterns and extent of wildlife roadkill in the Taiwan Roadkill Observation Network, a pinnacle of successful roadkill monitoring programs. This chapter provided insight on groups of importance for targeted roadkill mitigation in Taiwan as we found groups that were highly and disproportionately affected by roads, especially snakes. This first synthesis of all data from TaiRON provided an understanding of the magnitude of roadkill in Taiwan to inform conservation action. Understanding the patterns and magnitude of wildlife roadkill across the island allowed me to make an informed choice of study guilds and organisms from those that were found to be highly impacted for predictive roadkill risk modeling in following predictive roadkill risk modeling research.

In Chapter 3 I created predictive relative roadkill risk models across ecological scales for wildlife of conservation importance in Taiwan to inform targeted conservation action. I analyzed roadkill observations provided by TaiRON in a novel use of the SDM, MaxEnt, to predict relative roadkill risk across the Taiwan road network and identify high roadkill risk areas. My analyses also identified key environmental variables that impacted the roadkill risk for each guild and species modeled and quantified their contribution to risk. The models performed well across all studied ecological levels on a national scale and predictions and variable importance differed across guild and species models. This study demonstrated my predictive relative roadkill risk models are scalable to address the ecological question of interest and also emphasized the importance of systematic collection of roadkill data.

Finally, Chapter 4 focused on a particular species of conservation interest in a different landscape. Using modeling methodology based on those developed in Chapter 3, I created a predictive relative roadkill risk model for the Tasmanian devil (*Sarcophilus harrisii*) across the Tasmanian road network. I was interested in comparing the applicability of the predictive roadkill risk modeling methods to a juxtaposed landscape to expose the challenges for this methodology in other systems. Relative to Taiwan, Tasmania is sparsely populated by humans, has a low road density, and does not have as robust or established of a roadkill monitoring program. The species-specific model had fewer roadkill observations across a comparatively sparse road network, and new challenges of choosing ecologically relevant covariates for devils arose. The high model performance in predicting devil roadkill risk in this contrasting system suggests global applicability of the methodology, even when roadkill data is less abundant than from databases of larger programs.

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2. THE MAGNITUDE OF ROADKILL IN TAIWAN: PATTERNS AND CONSEQUENCES REVEALED BY CITIZEN SCIENCE[1]

2.1. Synopsis

Roadkill is among the most severe and insidious causes of impoverishment of vertebrate populations. As large roadkill databases develop, inferences from roadkill data can inform landscape-scale studies with broad con- servation aims. The Taiwan Roadkill Observation Network (TaiRON) is one of the largest roadkill databases, and we elucidated taxonomic, seasonal, and temporal trends of roadkill in Taiwan, as well as patterns of protected species roadkill. Notably, the study revealed that snakes were the largest proportion of all roadkill (35%) and 26% of snake roadkills were of protected species. Additionally, the top 23 species of a total 496 species ranked by roadkill abundance made up 50% of the observations. During winter, there were significantly fewer roadkill observations of bats, lizards, and snakes, but birds and mammals had fairly consistent roadkill across seasons. Additionally, 19% percent of the observations were of protected species. The staggering magnitude and extent of roadkill observations collected by TaiRON indicates a clear impact of roads of on Taiwan's vertebrate fauna. The patterns demonstrate that certain taxonomic groups are disproportionately killed on roads, and a small number of species account for most of the mortality. Additionally, certain seasons account for higher frequency of road kills, especially for ectothermic

[1] Reprinted with permission from "The magnitude of roadkill in Taiwan: Patterns and consequences revealed by citizen science" by Chyn, K., Lin, T.-E., Chen, Y.-K., Chen, C.-Y., & Fitzgerald, L. A., 2019. Biological Conservation, 237, 17-326, Copyright [2019] by Elsevier.

taxa. These are important insights, as this means that there are groups that are highly and disproportionately affected by roads. We hope this first synthesis of all data from TaiRON provides an understanding of the magnitude of roadkill in Taiwan to inform conservation action.

2.2. Introduction

The intersection of roads and wildlife is well-known to be ecologically hazardous (Forman & Alexander, 1998; Glista, DeVault, & DeWoody, 2008; Reeves, Dolph, Zimmer, & Tjeerdema, 2008; Trombulak & Frissell, 2000). Since the invention of automobiles, collisions have resulted in not only damages, injuries, and sometimes mortality of humans, but also include clearly-seen direct impacts of wildlife-vehicle collisions (WVCs) (Kroll, 2015; Shilling, Perkins, & Collinson, 2015), more commonly referred to as roadkill. Wildlife-vehicle collision events can be thought of as the unfortunate and obvious outcomes of a convergence of human transportation requirements and ecological systems. There are also lesser-witnessed indirect impacts of roads in surrounding landscapes. These areas that roads have ecological effects beyond the road itself is the 'road-effect zone' (Forman, 2000) and include effects such as the creation of barriers and filters to movement with associated reduction in dispersal and pollution (Andrews, Gibbons, & Jochimsen, 2006). However, as roads are necessary human infrastructure for the foreseeable future, we can salvage conservation benefit from data on existing roads and their effects to inform future planning and mitigation.

In 2013, >64 million km of paved and unpaved roads existed in the world (CIA, 2017), enough road length to circle Earth 1,604 times. Paradoxically, 80% of the planet remains roadless. However, when a 1 km buffer is applied to roads, roadless areas are fragmented into over 600,000 patches (Ibisch et al., 2016). Half of these roadless patches are <1 km^2, and consequently, many have low environmental value (Ibisch et al., 2016). Startlingly, the International Energy Agency estimates that an additional 25 million km of paved roads will be built by 2050, and that non-Organisation for Economic Co-operation and Development (OCED) countries will account for 90% of the growth (Dulac, 2013). The building of new roads in non-OCED nations will have large ecological impacts such as habitat loss, fragmentation, and habitat degradation (Laurance, 2015; Laurance, Goosem, & Laurance, 2009). Plans for future roads need to prioritize biodiversity conservation at all scales. For example, an important impact of roads is 'contagious' development, where roads "provide access to previously remote areas, thus opening them up for even more roads, triggering land-use changes, resource extraction, and human disturbance" (Selva, Switalski, Kreft, & Ibisch, 2015).

As a 40% increase in total road length is expected by 2050, it would be advantageous to survey existing roads for ecological data collection to inform future road building for the least impact on biodiversity. Roads are widespread and easily accessible but are often an untapped source of robust and widespread ecological data. One of the most visible forms of ecological data from roads is roadkill. Though there are an increasing number of localized studies of roadkill patterns (Hobday & Minstrell, 2008; Kioko, Kiffner, Jenkins, & Collinson, 2015; Maschio, Santos-Costa, & Prudente, 2016; Sosa & Schalk, 2016; Taylor & Goldingay, 2004), there is still a paucity of large organized databases of roadkill observations and larger-scale road ecology studies

(Shilling et al., 2015; van der Ree, Jaeger, van der Grift, & Clevenger, 2011; Waetjen & Shilling, 2017). Many of these studies are at the population and community scale, but there is a need to push towards landscape-scale research to inform conservation and mitigation on larger scales (van der Ree et al., 2011). As WVCs occur across landscapes and these observations are relatively easy to access and observe, large roadkill data collection programs, such as citizen-science roadkill observation projects, are invaluable to studying landscape-scale effects.

As large roadkill databases become more numerous and engaging for participants, the inference from this data will become more robust and can better inform a variety of landscape-scale studies with large temporal and spatial extents (Devictor, Whittaker, & Beltrame, 2010), such as wildlife distribution and monitoring (Hobday & Minstrell, 2008; Vercayie & Herremans, 2015) and hotspot and roadkill pattern studies (Gomes, Grilo, Silva, & Mira, 2008; Kioko et al., 2015; Seo, Thorne, Choi, Kwon, & Park, 2015). There are currently 12 large roadkill observation systems listed on https://globalroadkill.net (Shilling et al., 2015), a directory for roadkill databases and organizations that monitor roadkill. Most of these systems utilize volunteers or citizen scientists to collect observations and provide reliable data to inform road mitigation and planning (Waetjen & Shilling, 2017). We focus on one of the largest roadkill observation systems and databases, the Taiwan Roadkill Observation Network (TaiRON).

In the fall of 2011, a coalition of concerned citizens spearheaded by Te-En Lin, a zoologist at the Taiwan Endemic Species Research Institute (TESRI), started a Facebook (TM) group that noted and discussed the daily roadkill they encountered in Taiwan. This small group quickly garnered interest from the public and evolved into a thriving, government-funded, national citizen science project and one of the largest roadkill observation systems in the world (Waetjen & Shilling, 2017). Since 2011, the Taiwan Road Observation Network (TaiRON) has captured national media attention, membership has expanded rapidly, and the collection and database systems are consistently updated to keep up with the increased interest and data management demands. Citizen scientists are provided with in-person training around the nation, equipment and TaiRON paraphernalia, and a web application (webapp) accessible across smartphone platforms (https://roadkill.tw/en/app/report). Volunteers are also encouraged to submit carcasses in good condition to be made into specimens at the TESRI collection. Project managers employ adaptive management by continuously monitoring data quality and quantity and corresponding with volunteers, researchers, and transportation managers to assess project satisfaction and to address concerns. Additionally, interested parties need only to register on the website to gain access to the dearth of roadkill data for non-protected species, whereas no other program makes data so readily accessible to users, even citizen scientist contributors. The objectives of TaiRON are to promote public and decision-maker engagement and understanding, mitigate WVCs to reduce impact on wildlife, and to utilize the data to gain better understanding of regional biodiversity. To achieve these goals, we have collaborated with citizen scientists to conduct broad opportunistic roadkill surveys and provided regular feedback to the public, media, and government. We believe these are aspects of

TaiRON that stand out among other roadkill observation programs, especially given its nationwide scale of participation and comparatively large database.

Taiwan, an island with high ecological value (Laurance et al., 2014) and high road density is thus an ideal site for our study. Myers et al. (2000) states that Taiwan "appear[s] to feature exceptional […] endemism and exceptional threat, but are not sufficiently documented", so biological data collection is applicable and necessary for this ecologically valuable island. Additionally, Taiwan already has twice the road density of the U.S.A. at 1.2 km/km^2 and 0.67 km/km^2, respectively (CIA, 2017). Due to Taiwan's ecological value and high road density, we are motivated to bring attention to this incredible source of ecological data of which there have been no publications on baseline statistics. We address this gap by conducting analyses to elucidate the ecological trends and patterns of roadkill in Taiwan. Previous studies have shown roadkill observations to be higher for ectotherms (Farmer & Brooks, 2012) than other taxa, seasonality in roadkill richness and rates (da Rosa & Bager, 2012), and differences in roadkill composition of nocturnal and diurnal species (Kioko et al., 2015). We expected ectotherms, particularly snakes, would incur the highest levels of roadkill due to their need for thermoregulation, which may attract them to warm roads (Andrews, Gibbons, Jochimsen, & Mitchell, 2008) and their tendency for immobilization behavior in response to oncoming traffic (Andrews, Gibbons, & Reeder, 2005). Wildlife activity also varies with seasonal patterns, which has been correlated with rates of roadkill (da Rosa & Bager, 2012; Shepard, Dreslik, Jellen, & Phillips, 2008), and we predicted warmer seasons of spring and summer to have the highest levels of road mortality observations across taxa, but especially in ectotherms. To address these questions, we analyzed TaiRON data and test for differences in magnitude of roadkill among taxonomic groups, across seasons, and by activity pattern of the top 20 roadkilled species. We also quantified the trends and patterns of roadkill of protected species.

The TaiRON data is opportunistic roadkill data and is one of the most extensive and complete vertebrate occurrence point data sets in Taiwan, and one of the most extensive roadkill databases in the world. This work is the first synthesis of patterns and trends of the TaiRON roadkill observation dataset. As an important first step towards understanding the complexities of WVCs in Taiwan, insights from our analyses will allow us to gain a fuller understanding of the ecological impacts roads pose to wildlife to inform future analyses and possible conservation action. Our study also highlights the value of large roadkill databases for developing conservation strategies.

2.3. Methods

2.3.1. Study System

Taiwan is a Pacific island roughly 180 kilometers off the south-eastern coast of mainland China that emerged due to collision of the Philippine Sea plate and the Eurasian plate during the Mio-Pliocene boundary (Adler, HilleRisLambers, & Levine, 2007). During the Pleistocene, glaciation and land bridges between China and Taiwan provided opportunities for colonization and isolation of organisms in Taiwan (T.-Y. Chiang & Schaal, 2006; Y.-C. Chiang, Huang, & Liao, 2012), and present day biota is expected to have originated from Asia and surrounding islands (Ali, 2017; He, Gao, Su, Lin, & Jiang, 2018). As Taiwan is located at the border of the Palearctic and Oriental biogeographic zones and contains large elevational heterogeneity, it contains diverse habitats that support high biodiversity (He et al., 2018) and over 9079 faunal species (Center, 2018). Taiwan's total area is 36,193 km^2, and the climate is subtropical in the North to tropical in the South. The human population of Taiwan is approximately 23 million people, comparable to the population of the continent of Australia (CIA, 2017). Taiwan is incredibly biodiverse but also space and resource-limited, making roads and associated removal of habitat more detrimental to faunal populations.

2.3.2. Data

Data for this study were obtained from the Taiwan Roadkill Observation Network (TaiRON) database of citizen science collected roadkill data (https://roadkill.tw). Data is extensive and opportunistically collected, and volunteers contribute data from throughout Taiwan. Though the database contains roadkill observations prior to 2011, the citizen science project led by zoologists at the Taiwan Endemic Species Research Institute (TESRI) was officially formed in 2011. The Taiwan Road Observation Network uses social media (Facebook) to both collect data and engage participants, and TaiRON project managers are continuously improving its data collection methodology and citizen science engagement practices. Currently, data is mainly collected and uploaded to the TaiRON database via a web application (https://roadkill.tw/en/app/report) created by data science collaborators. The communal data workflow and web-based systems for the acquisition and management of roadkill observations were designed and implemented by a group of information scientists and biodiversity researchers at Academia Sinica in Taipei, and the data workflow and information system is a crucial component in the successful aggregation of diverse, high-quality, and large-volume observations (Chuang et al., 2016). Project managers then verify individual "unconfirmed" observations for accuracy, which are then either marked as "confirmed" or "unable to confirm." Observations are marked as "confirmed" when consensus is reached on taxonomic identification and locational and date/time data are provided. Data on non-protected species is freely available to the public for live download, whereas protected species and participant data is only available to those who have approved applications.

For this study, the full dataset, including protected species observations and data contributed from the Freeway Bureau, Ministry of Transportation and Communications Taiwan, was downloaded from TaiRON on 9 March 2018, and at the time of download contained a total of 101,354 geo-referenced observations (Fig. 2.1) spanning years 1995-2018 with the bulk of the data (85%) from 2011 onwards (Fig. 2.2). Additionally, protected area data was downloaded from Taiwan's governmental open data repository (https://data.gov.tw/en).

2.3.3. Analysis

We removed records prior to 2011 and included only confirmed observations for this analysis. Confirmed observations were those that had been checked by TaiRON staff scientists. We also calculated survey effort (observations/participants) for each full year of data (2012-2017) (Fig. 2.2) and compared the number of observations with the number of participants for each year (Fig. 2.2) with a Spearman correlation test, as the our data did not meet the assumptions for a Pearson's correlation test. For this study, taxonomic, locational, temporal, and participant attributes of the data were analyzed. We analyzed only vertebrate groups which comprised 92% of the confirmed observations with biological data such as genus, species, family, or major taxonomic group. All vertebrate observations were classified to the following major taxonomic groups: bats, birds, frogs, lizards, snakes, turtles, and terrestrial mammals. Bats were treated as a separate group as all other mammals were terrestrial mammals. Herpetofaunal groups were separated due to large differences in numbers of observations across taxonomic groups. The final dataset contained 45653 observations for analysis (Fig. 2.1).

Additional sorting of the data was performed for analyses on road type, protected species, and seasonality. Roads in Taiwan are classified into four main types and one miscellaneous category, and we conducted descriptive analyses and ANOVAs on the roadkill by road type and major taxonomic group road data was acquired from the GIS-T Transportation Network Geographic Information Storage System: Taiwan Ministry of Transportation and Communication (Tao & Hung, 2013). We used the Taiwan's Wildlife Conservation Act pre-25 June 2018 protected species list (Bureau, 2016) for our analyses on observed protected species. Seasonal analyses were performed by sorting the observations into the following seasonal categories: observations falling between December – February were designated as "winter," March – May were designated as "spring," June – August were designated as "summer," and September – November were designated as "fall." Subdivisions for seasonal analysis correspond with seasonal and biological cycles in Taiwan.

We performed ANOVAs to test for differences in mean number of roadkill observations across seasons and road types. Separate analyses were conducted for each major taxonomic group as some groups required non-parametric tests. To test for heteroscedasticity, we performed Levene's tests on the number of observations per season for all major taxonomic groups. All groups met the assumptions of ANOVA, including independence, normality, and homogeneity of variances (indicated by Levene's test) except for bats. That is, the number of bat WVC observations had unequal variances across seasons and violated the homogeneity of variance assumption needed for an ANOVA, so we conducted a Kruskal-Wallis test for bats as a non-parametric alternative. We also performed all tests with outliers removed and results of significance did not change. We chose to report results of analyses with the original data because the outliers were not due to inaccuracies in data and did not change resulting outcomes. We used the program R (version 3.4.0) (Team, 2017) for our analyses.

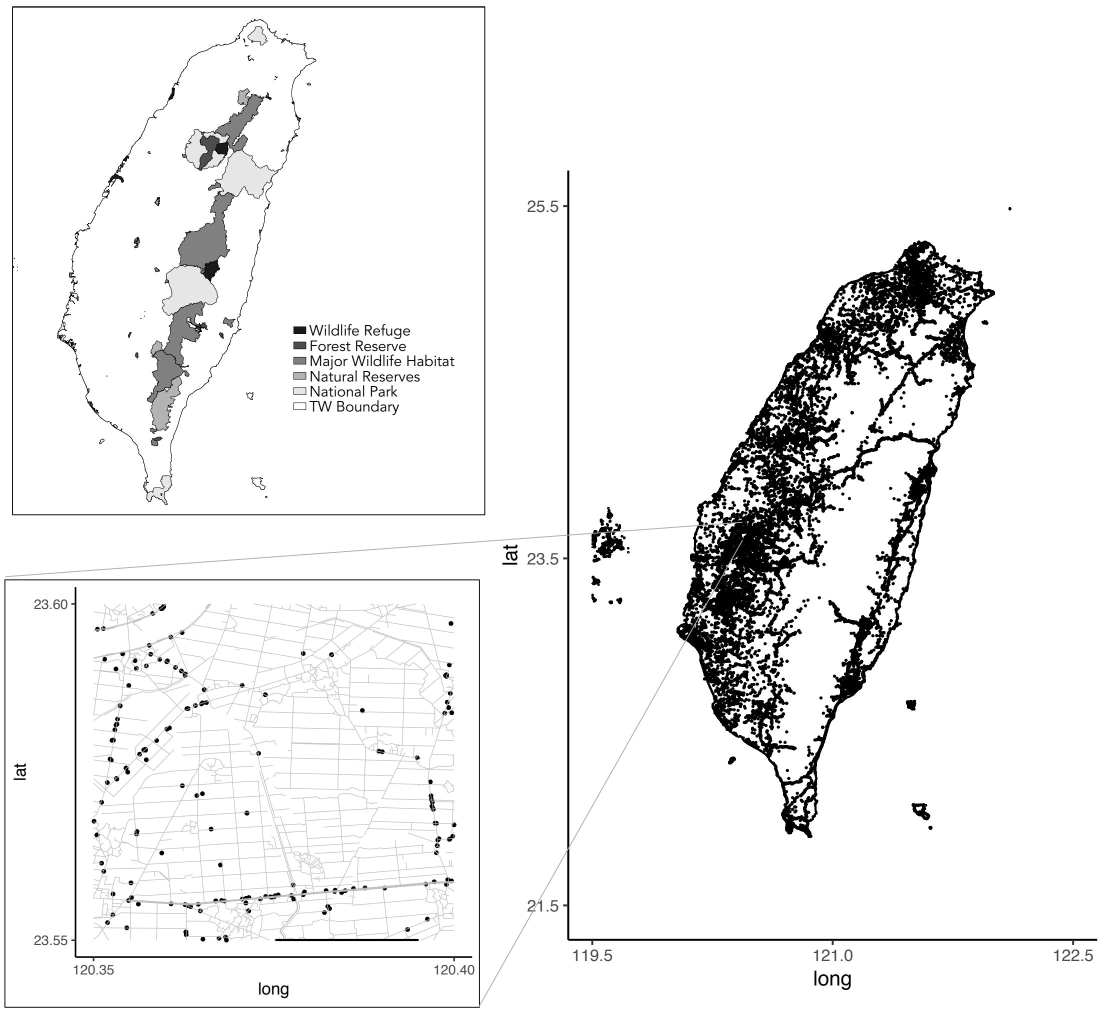
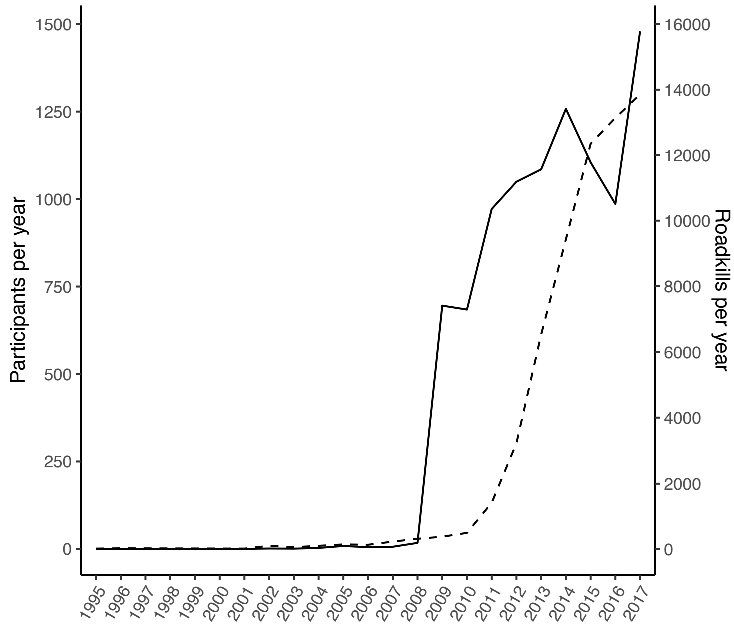


Figure 2.1 Map of Taiwan with outlying islands, showing the 45,653 TaiRON roadkill observations (black points) that were used for analyses. The upper inset shows a map of protected areas (in shades of gray) in Taiwan. Most protected area coverage is within the steep and rugged terrain of Taiwan's Central Mountain Range which has remained largely roadless. The lower inset is an example of roadkill observations (black points) plotted in a 5 km2 area against the network of roads in gray.



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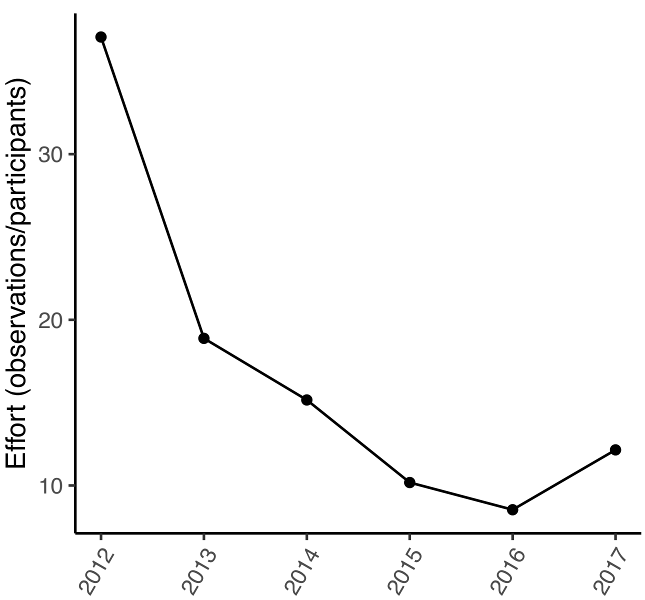


b)

Figure 2.2 The number of TaiRON participants per year in dashed line and the number of roadkill observations per year in the solid line. 2018 are data omitted due to incomplete data for the year. TaiRON officially began in September 2011. b) Survey effort measured as observations/participant per full year of data showed a decreasing trend from years 2012–2017.

2.4. Results

2.4.1. Participation

There were 3414 unique TaiRON participants from 2011 – 2018. The number of participants increased from 302 contributing participants in 2012 to 1299 contributing participants in 2017. Observations of roadkill also increased dramatically during this period (Fig. 2.2) and was significantly correlated ($r = 0.79$, $p < 0.0001$). However, effort measured as observations/participant showed a decreasing trend from 2012 – 2017 (Fig. 2.2).

2.4.2. Taxonomic Diversity and Prevalence of Roadkill

The 45653 vertebrate roadkill observations comprised 109 families, 294 genera, 496 identified species. Of the major vertebrate taxonomic groups, snakes comprised the largest proportion of the data with 15963 roadkill observations (35%). Birds were the second most observed group with 11238 of roadkill observations (25%), followed by frogs (7900 roadkill observations, 17%), mammals (5921 roadkill observations, 13%), lizards (3457 roadkill observations, 8%), turtles (740 roadkill observations, 2%), and lastly bats (434 roadkill observations, < 1%) (Fig. 2.3).

A rank abundance curve showed a skewed distribution where a small number of the total 496 species made up of the majority of roadkill observations (Fig. 2.4). The top 23 species ranked by roadkill abundance made up 50% of the observations and the top 79 species encompassed 75% of the observations. The top 20 most-observed roadkill species made up 47% of all observations ($n = 23217$). Among the top 20 most-observed roadkilled species, 13 are nocturnal (65% of the top 20 observed roadkill species), 6 are diurnal (30%), and 1 is cathemeral (5%) (Table 1).

2.4.3. Road Type

Proportionally, the type of road on which most roadkill observations were found per 100 km (to account for the length of road per road category) was on county highways (Fig. 2.5). There was no statistical difference in mean WVC observations across road types in each major taxonomic group [bats: $F_{(3, 27)} = 0.56$, $p > 0.05$ for all groups; birds: $F_{(3, 28)} = 0.59$, frogs: $F_{(3, 28)} = 1.47$; lizards: chi-squared = 4.6782, df = 3; mammals: $F_{(3, 28)} = 0.13$; snakes: $F_{(3, 28)} = 1.17$; turtles: $F_{(3, 26)} = 1.355$].

2.4.4. Protected Species

Of the 496 observed species, 96 (19%) are listed as protected by the Taiwanese government in accordance to Taiwan's Wildlife Conservation Act (Bureau, 2016; Center, 2018). As the data were downloaded prior to the minor changes made on 25 June 2018, we are using the pre-25 June 2018 list of protected species for analysis (Bureau, 2016). The top three protected species with the highest number of observations were snakes, and the three protected snake species encompassed 50% of the 6193 protected species observations. Thirteen percent of the total confirmed roadkill observations were protected species.

Notably, roadkill observations included 100% of protected terrestrial (non-marine) turtle species, 94% of protected terrestrial snake species, 86% of the protected lizard species, 76% of protected mammal species, and 50% of both protected bird and bat species in Taiwan (Bureau, 2016; Shao et al., 2007) (Table 2).

In particular, protected snakes had alarmingly high numbers of roadkill, as they were the top three most observed roadkilled species, which encompassed half (50%) of the protected species observations. These snakes are: Taiwan Habu (*Protobothrops mucrosquamatus)* (1480 obs., 24% protected species observations, #4 most observed roadkill species), Many-banded Krait (*Bungarus multicinctus multicinctus*) (1210 obs., 19% protected species observations, #9 most observed roadkill species), and Chinese Cobra (*Naja atra*) (414 obs., 7% protected species observations, #28 most observed roadkill species). Additionally, protected snake species accounted for 26% of total snake observations.

2.4.5. Variation in Roadkill

We found that all groups, except for bats (F = 6.1049, p = 0.0044) and lizards (F = 3.0299, p = 0.0533), passed the Levene's test for homogeneity ($p < 0.05$). There were statistically significant differences ($p < 0.05$) between seasonal means for snake ($F_{(3, 26)}$ = 7.19, p = 0.0011) WVC observations. The Kruskal-Wallis test revealed statistically differences between seasons for bat roadkill (chi-squared = 8.6212, df = 3, p-value = 0.0348) and lizard roadkill (chi-squared = 12.639, df = 3, p-value = 0.0055). All other groups did not have statistically significant differences between seasonal WVC means [birds: $F_{(3, 20)}$ = 0.136, $p > 0.05$ for following groups; frogs: $F_{(3, 20)}$ = 0.983; mammals: $F_{(3, 20)}$ = 0.672; turtles = $F_{(3, 19)}$ = 1.673]. In summary, there were fewer roadkill observations in winter and spring (Fig. 2.6). There was an overall decrease in roadkill observations during winter (Fig. 2.6) and there were significantly fewer roadkill observations in bats, lizards, and snakes. Birds and mammals had fairly consistent roadkill counts across seasons (Fig. 2.7).

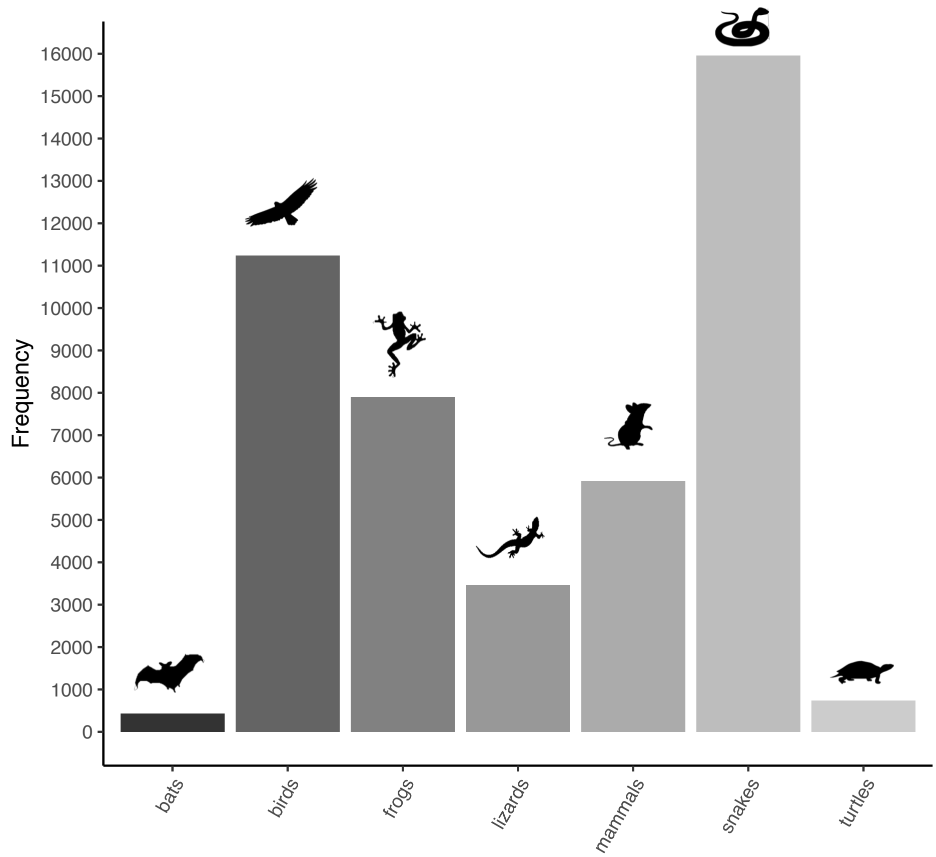
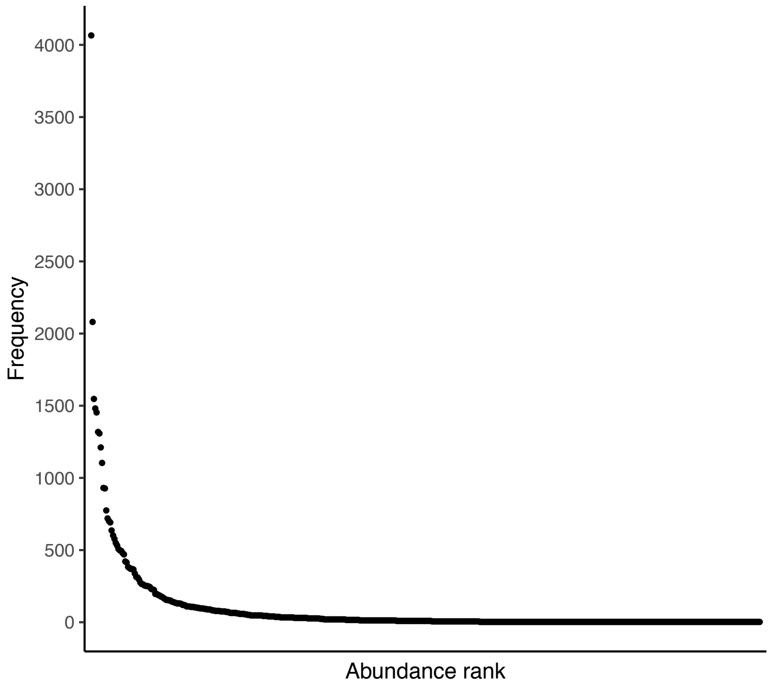


Figure 2.3 TaiRON vertebrate roadkill observations by major taxonomic group from 2011 to 2018.



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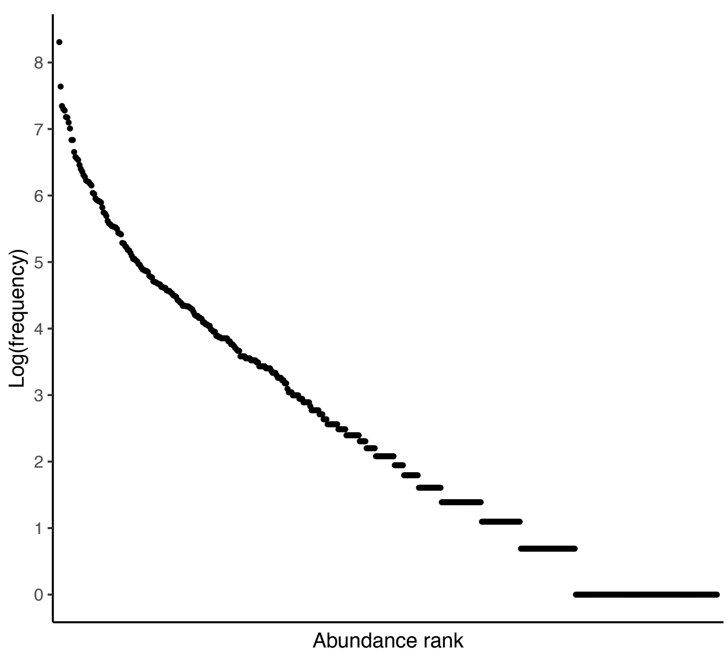

b)

Figure 2.4 a) Rank abundance curve of species roadkill frequencies from highest frequency to lowest frequency (from left to right); b) Log of rank abundance of species frequencies from highest frequency to lowest frequency (from left to right).

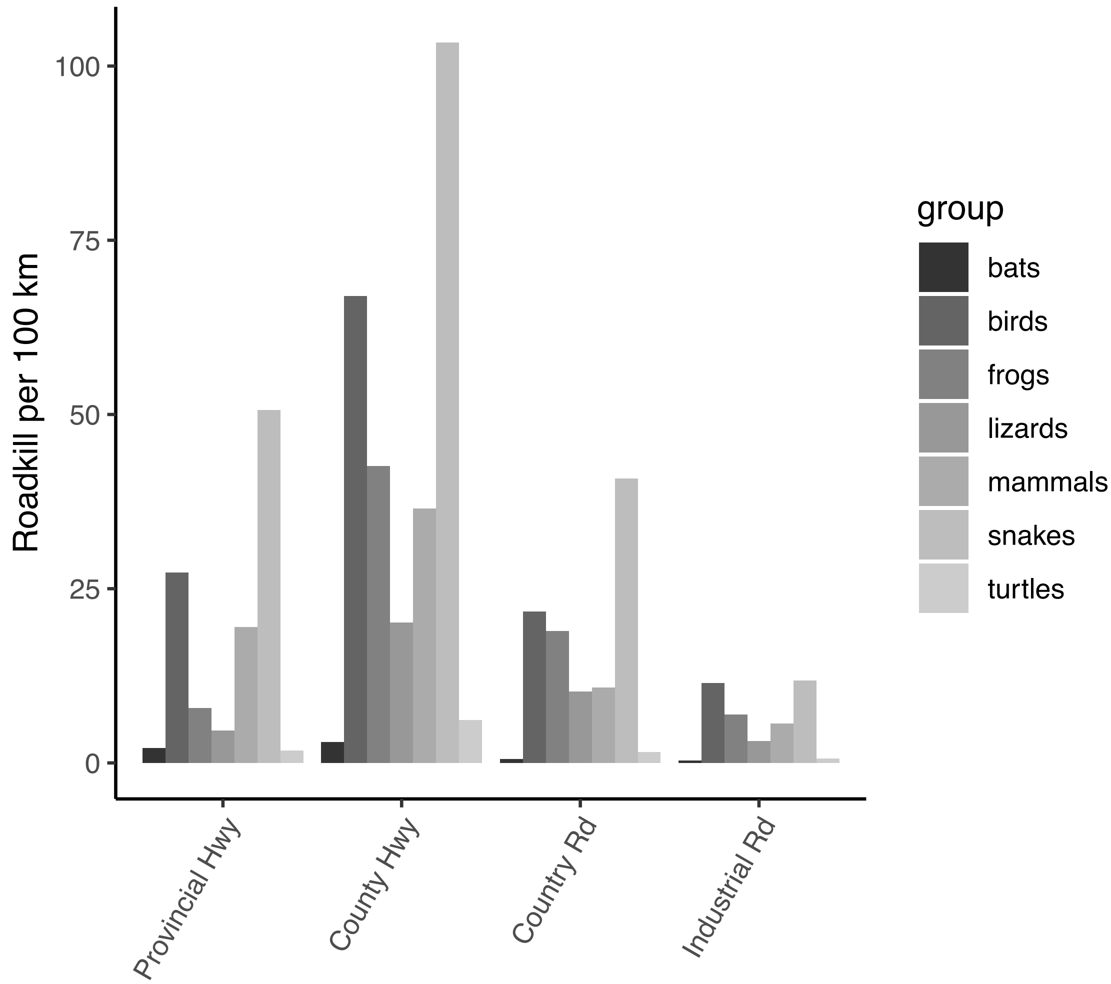

Figure 2.5 Proportional frequencies of roadkill per 100 km of road (to account for the length of road per road category) for Provincial Highway, County Highway, Country Road, and Industrial Road (from left to right).

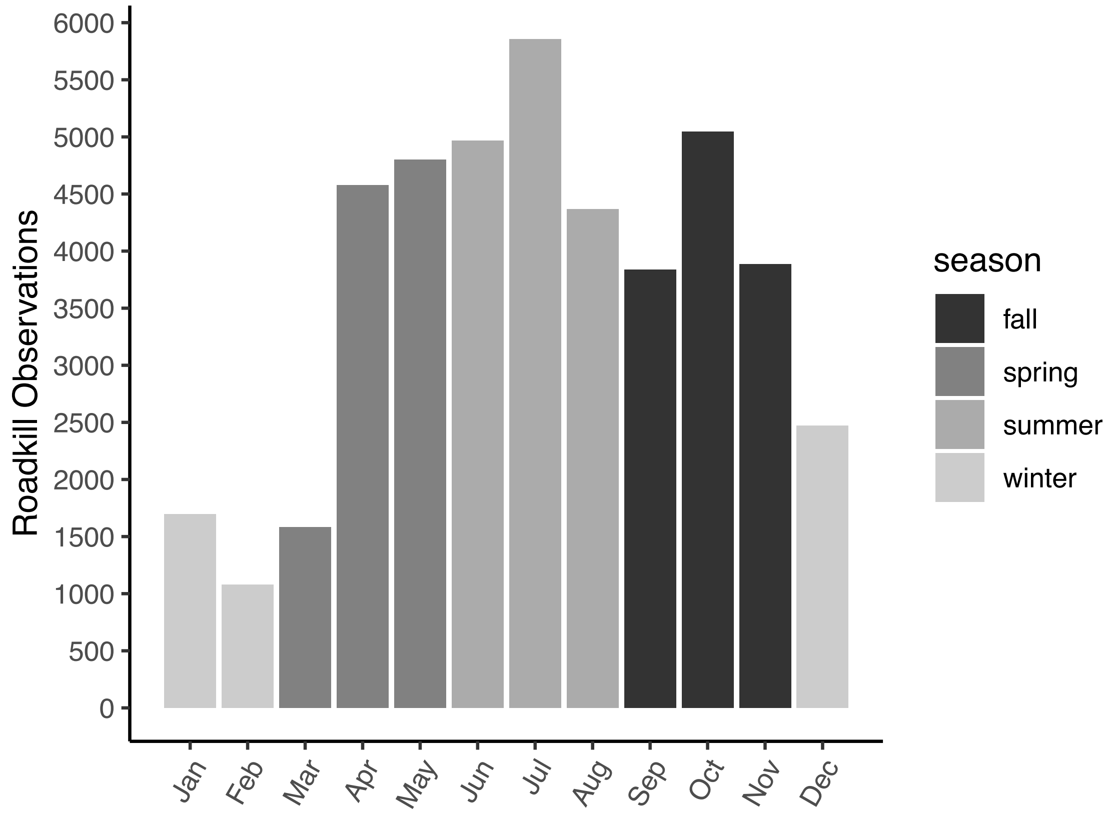

Figure 2.6 Aggregated TaiRON vertebrate roadkill observations per month from 2011 to 2018.

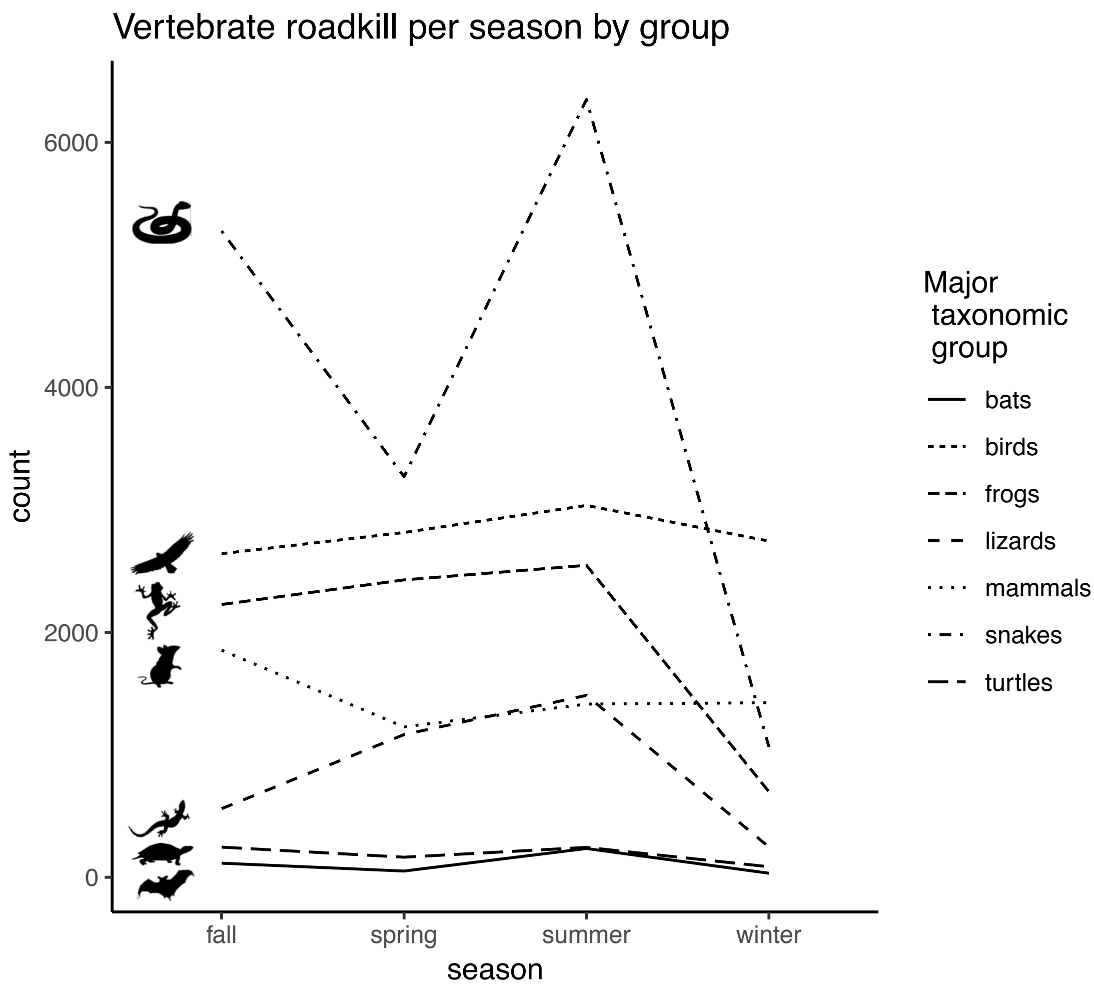

Figure 2.7 Aggregated seasonal TaiRON roadkill observations from 2011 to 2018 per major taxonomic group.

Table 2.1 Top 20 observed roadkill species from 2011 - 2018, their major taxonomic group, the number of observations, their activity period behavior, and the number of observations per season.

Species	Group	N	Activity	Fall	Spring	Summer	Winter
Duttaphrynus melanostictus	frogs	4067	Nocturnal	1152	1316	1328	271
Cyclophiops major	snakes	2081	Nocturnal	532	421	1067	61
Passer montanus saturatus	birds	1547	Diurnal	351	467	482	247
Protobothrops mucrosquamatus	snakes	1480	Nocturnal	548	278	364	290
Streptopelia tranquebarica huminis	birds	1452	Diurnal	414	230	334	474
Japalura swinhonis	lizards	1318	Diurnal	138	476	673	31
Boiga kraepelini	snakes	1309	Nocturnal	385	288	589	47
Bungarus multicinctus multicinctus	snakes	1210	Nocturnal	457	154	525	74
Lycodon rufozonatus rufozonatus	snakes	1105	Nocturnal	331	250	470	54
Trimeresurus stejnegeri stejnegeri	snakes	931	Nocturnal	531	133	189	78
Melogale moschata subaurantiaca	mammals	928	Nocturnal	328	254	136	210
Oligodon formosanus	snakes	775	Nocturnal	77	151	543	4
Ptyas mucosus	snakes	718	Diurnal	325	136	222	35
Bufo bankorensis	frogs	703	Nocturnal	191	246	89	177
Rattus norvegicus	mammals	691	Nocturnal	190	109	173	219
Suncus murinus	mammals	637	Nocturnal	243	106	171	117
Lycodon ruhstrati ruhstrati	snakes	601	Nocturnal	160	144	244	53
Amphiesma stolatum	snakes	579	Diurnal	182	176	201	20
Elaphe carinata	snakes	551	Cathemeral	278	114	132	27
Pycnonotus sinensis formosae	birds	534	Diurnal	81	234	156	63
Total		23217		6894	5683	8088	2552

Table 2.2 Statistics on the total number of terrestrial vertebrate species in Taiwan and percent of those species observed in the roadkill dataset, the number of protected terrestrial vertebrate species in Taiwan and the percent of those species observed, and N per taxonomic group and the percent of N that is of a protected species.

Group	Total species	% total species roadkilled	Protected species*	% protected species roadkilled	Total N	% N protected species
Bats	37	56.76	2	50.00	434	1.15
Birds	659	43.85	90	53.33	11238	10.08
Frogs	36	86.11	7	85.71	7900	0.90
Lizards	40	95.00	7	85.71	3457	2.98
Mammals (land)	52	98.08	17	76.47	5926	10.95
Snakes	49	100.00	17	94.12	15963	26.21
Turtles	5	100.00	3	100.00	779	17.07
Total	878	NA	148	NA	45697	NA

* pre 25 June 2018

2.5. Discussion

The staggering magnitude and extent of roadkill observations collected by TaiRON indicates a clear impact of roads of on Taiwan's vertebrate fauna and demonstrates the importance of focused effort on further study and mitigation for WVCs in Taiwan. Between fall 2011 and spring 2018, TaiRON collected 45653 verified geo-referenced vertebrate observations, and this number is likely a vast underestimate of the true amount of roadkill in Taiwan due to ecologically-sourced, observer-sourced, and environmentally-sourced biases, explained below. Roadkill is pervasive on Taiwan and occurs throughout the island except in the largely roadless high elevation Central Mountain Range. These areas also coincide with protected areas (Fig. 2.1), but do not attribute the lack of roadkill in these areas to the effectiveness of protected areas in preventing or decreasing roadkill, but to the fact that Taiwan's Central Mountain Range is extremely steep and rugged, so roads are not easily built and the area is not easily accessible for human settlement.

Notably, the patterns of roadkill demonstrate that certain taxonomic groups are disproportionately killed on roads, and that a small number of species account for most of the roadkill. Additionally, certain seasons account for higher frequency of road kills, especially for ectothermic taxa (e.g. reptiles & amphibians). These are important insights, as this means that there are groups and species that are being highly and disproportionately affected by roads.

With the advent of smart-phone collected citizen science data, databases of readily available and accessible wildlife data, such as roadkill observations, will become increasingly important for conservation. Additionally, the predicted 40% increase in total global road length by 2050, makes citizen science programs and roadkill data collection systems like TaiRON indispensable for utilizing existing roads for ecological data collection. These programs can offer data to inform this increase in future road building to have the least impact on biodiversity and wildlife. Though this field of roadkill data collection is growing, there is still a paucity of large organized databases of roadkill and larger-scale road ecology studies (Shilling et al., 2015; van der Ree et al., 2011; Waetjen & Shilling, 2017). As WVCs occur across landscapes and these observations are relatively easy to access and observe, we believe large landscape-scale roadkill data collection programs, such as TaiRON, are invaluable to studying landscape-scale effects.

The dramatic increase of TaiRON citizen science participants from 2012-2017 was correlated with the increase of roadkill observations, and the large number of new participants explains the higher number of observations every year (Fig 2.2a). However, the effort of participants (observation/participants) per year dropped dramatically after 2012, likely due to the increase of participants that contributed fewer observations of roadkill (Fig 2.2b).

Snakes were the most reported roadkill in Taiwan with 35% of total confirmed observations. This may be due to the behavior of snakes that enhance the probability of wildlife-vehicle collisions, human behavior in response to wildlife on roads, observation bias, or a mixture of causes. Certain ecological traits of snakes such as body size, movement speed, thermoregulation behavior, and feeding behavior may also affect the probability of wildlife-vehicle collisions (Andrews et al., 2008; Andrews et al., 2005; Langen, Ogden, & Schwarting, 2009). For example, some snakes have been observed to have an immobilization response on roads when a vehicle approaches, which may increase their risk of being struck by a vehicle (Andrews et al., 2005). Snakes have also been noted to bask on roads for thermoregulation, which makes them more vulnerable to WVC (Andrews et al., 2006; Bernardino Jr & Dalrymple, 1992; Klauber, 1939). Additionally, several studies reported drivers intentionally colliding with wildlife, notably snakes, on roads, which could also contribute to the reported high proportion of snake roadkill observations (Ashley, Kosloski, & Petrie, 2007; Crawford & Andrews, 2016; Secco, Ratton, Castro, da Lucas, & Bager, 2014), though there have been no studies on intentional WVC behavior in Taiwan. Lastly, observation bias may also be a source of high reported snake roadkill. Due to size, many smaller animals such small mammals (rodents), amphibians (frogs & toads), and lizards may be underreported, while larger and longer animals, such as snakes, mammals, and birds, may be more easily seen and reported. Additionally, most roadkill was concentrated on a small number of species (the top 23 species accounted for 50% of the roadkill observations). These findings indicate that targeted mitigation strategies for snakes and top roadkill species should be seriously considered.

Additionally, 13 of the top 20 most roadkilled species are nocturnal. As noted in the results, a high proportion (65%) of the top 20 roadkill species (53% of all vertebrate roadkill) were nocturnal. This may be due to several factors including reduced driver vision at night, which may shorten the time a driver has to react to an animal on the road, and the proportion of animals active at night. Additionally, 20% of faunal species in Taiwan are nocturnal (Center, 2018), which may contribute to a higher likelihood of collision with an animal during this activity period. Additionally, wildlife may be blinded or stunned by the light of passing vehicles. However, mitigation measures should be tested while keeping other ecological effects in mind; e.g. strategies such as increased lighting may increase driver vision, but may have other ecological impacts, especially for nocturnal animals (Baker & Richardson, 2006; Bird, Branch, & Miller, 2004; Buchanan, 1993; Macgregor, Pocock, Fox, & Evans, 2015).

The database also provides a wealth of ecological information on protected species (13% of the total roadkill observations were indicated as protected species) that are often difficult to study and collect in Taiwan, likely due to both low detection rates and governmental restrictions on protected species research. Additionally, at the time of data download, TaiRON citizen science volunteers collected 5528 specimens of protected species, which are scientifically valuable and were preserved and stored at TESRI. The most WVC-impacted group of protected species was the snake group, as snakes accounted for half of the protected species observations. We believe conservation research and mitigation efforts should be focused on these protected species with observed high roadkill observations. This invaluable protected species data can be used to supplement ecological studies lacking in data, such as distributional studies on cryptic and rare species.

As most ectothermic species and species that hibernate have reduced activity in the winter months, it was expected there would be fewer roadkill observations during this season (Farmer & Brooks, 2012). Bats, lizards, and snakes differed significantly in WVC observations across seasons, likely due to ecological changes in seasonal activity. The seasonal difference in roadkill could allow for seasonal mitigation efforts rather than yearlong action. This seasonal activity pattern could reduce conservation spending and provide more targeted conservation action. For example, mitigation could be implemented during seasons with high activity, breeding, or migration seasons, which is ecologically directed and seasonal rather than year-round.

TaiRON citizen science data was collected opportunistically, and it contains presence only data. There are ecologically-sourced, observer-sourced, and environmentally-sourced biases. Ecologically-sourced biases may include effects of body size, color of wildlife, and persistence of roadkill on roads before decomposition or scavenging. These factors may introduce variability in likelihood of WVCs and detection. For example, bias may also occur when there is a difference in persistence of roadkilled animals on roads; soft bodied and smaller bodied animals may be removed at higher rates, which would make detection of the animals more difficult (Ratton, Secco, & Da Rosa, 2014; Santos, Carvalho, & Mira, 2011; Teixeira, Coelho, Esperandio, & Kindel, 2013). Observer-sourced biases may include effects of traveling speed, traveling method, and perceived danger of data collection. Differences in traveling methods (driving instead of walking) have been associated with a decrease the detection rate of roadkill (Langen et al., 2007), likely caused by an increase of traveling speed. Additionally, perceived danger of data collection due to traffic or road conditions may deter citizen scientists from stopping for roadkill on certain roads. Additionally, environmentally-sourced biases may include effects of weather conditions and environmental stochasticity. Environmentally-sourced conditions may deter participants or obscure detection of roadkill data.

This study gives researchers baseline context to inform future research utilizing this data on an island with high biodiversity and endemism. Species on islands have the highest risk of extinction, and "reptiles on islands also risk extinction by chance alone due to their isolation and small areas of occupancy" (Fitzgerald et al., 2018). As 86% of documented reptile extinctions have been on tropical islands (Fitzgerald et al., 2018; IUCN, 2019), the consequences of high road mortality for reptiles, especially snakes, in Taiwan could be grave.

We have found patterns among the roadkill data and elucidated the importance of focusing mitigation and research effort on protected snakes and nocturnal animals in Taiwan. Such mitigation actions can include building culverts and passages for wildlife (Smith, Van Der Ree, & Rosell, 2015), fencing along sections of road with high mortality (van der Ree, Gagnon, & Smith, 2015), animal detection systems (Huijser, Mosler-Berger, Olsson, & Strein, 2015), and reduction in vehicle speed. As Taiwan is experiences frequent infrastructural and road destruction by way of natural disasters (typhoons and earthquakes), we propose that Taiwan uses these destructive events as an opportunity to rebuild roads with mitigation strategies incorporated, especially mitigation that will aid in reduction of snake road mortality (culverts and fencing).

Due to the high amount of data on protected species (over 6000 records), TaiRON can also provide an important source of data on the life history, ecology, and distribution of cryptic and/or rare species as many cryptic species are lacking in basic ecological data. TaiRON also serves as a source of collection specimens and has already informed research outcomes with major implications for the public. TaiRON has been utilized to inform not only transportation planning and mitigation for wildlife, but also topics of importance to public health. In 2013, TaiRON provided several Taiwan Ferret Badger (*Melogale moschata subaurantiaca*) roadkill specimens collected by citizen scientists for analysis that helped confirm the presence of rabies in Taiwan. This was a weighty public health matter because rabies was previously thought to be absent on the island. Epidemic analyses on carcasses provided by TaiRON helped reveal that rabies had specialized into a RABV-TWFB strain in Taiwan, and that it had differentiated on the island 158 to 210 years ago (Chiou et al., 2016). This important and practical application of data and specimens gathered by TaiRON volunteers has further made this group indispensable to public, scientific, and governmental sectors in Taiwan and internationally.

As only a small fraction of all roadkill is observed, future work can be aimed at using TaiRON to attain more robust estimates of the actual roadkill extent. Important next steps are to conduct more in-depth spatial analyses on the TaiRON data, as well as establishing systematically citizen science data collection to help reveal the biases inherent to opportunistic citizen science data. Spatially explicit analyses were not included in this study because roadkill is prevalent throughout Taiwan except for the roadless high mountain areas (Fig. 2.1), and these types of analyses, which would include in depth discussion of environmental correlates, are appropriate for a different paper, which we are preparing. Moreover, spatial analyses like a hotspot analysis would not enhance our discussion of the vulnerability of taxon groups, risk of roadkill across seasons, and impact on protected species. As roadkill is pervasive throughout Taiwan, it is meritorious and important to describe the magnitude of roadkill and parse out the degree of roadkill among taxonomic groups, by season, and how roadkill impacts protected species. Future work can focus on modeling roadkill risk for specific species and groups, as well as conducting studies on the detection biases of voluntary and opportunistic roadkill data collection. As TaiRON has access to a large engaged group of citizen science participants, future studies can also explore participant demographics and the effects of participation on environmental literacy (Hsu, Lin, Fang, & Liu, 2018). The TaiRON database provides ample opportunity for further future research to explore a wide spectrum of spatial, temporal, and citizen science participant studies.

The Taiwan Roadkill Observation Network is a unique and valuable project due to its scope, adaptive management style, and level of engagement from its volunteers (>3,400) and managers. Its reach extends far beyond roads and wildlife and has made major contributions to public health and has made citizen engagement in science easily attainable in Taiwan. TaiRON and its database have and will continue to provide important conservation information about the impacts of human activity and pressures associated with roads on wildlife biodiversity.

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3. THE INTERSECTION OF WILDLIFE AND ROADS: FINE-SCALE ROADKILL RISK MODELS FOR HERPETOFAUNAL GUILDS AND SPECIES OF CONSERVATION CONCERN IN TAIWAN

3.1. Synopsis

3.1.1. Aim

Robust, spatially-explicit approaches accounting for ecological drivers are needed to gain insight into environmental correlates of roadkill and set conservation priorities. We modeled and predicted wildlife road mortality across a nation-wide road network using species distribution models (SDMs) and environmental covariates for informing conservation action.

3.1.2. Location

Taiwan is the location of the study.

3.1.3. Methods

We applied the MaxEnt SDM to a large citizen science database of >60,000 roadkill occurrences to predict the probability of roadkill for herpetofaunal guilds of conservation need. Twenty-eight environmental covariates at 50 m spatial resolution were included, such as road type, road width, and 26 land cover composition and distance variables. Models were created for the following guilds and species: Common Venomous Snakes (CVS), Semiaquatic and Aquatic snakes (SAS), and Turtles with k=10 cross-validation, and both k=10 and k=50 cross-validation for the Maki's keelback snake (*Hebius miyajimae*, HM). We used the AUC model evaluation metric and minimum and 10th percentile training presence threshold omission rates to help assess model performance. Intuitive interactive roadkill risk maps were developed for conservation practitioners.

3.1.4. Results

All predictive models performed well and had AUCs >0.7. Important covariates among the differing roadkill models included road width, road type, buildings, rice, and fruit trees. Projected roadkill risks for CVS, SAS, turtles, and HM were highest in montane regions, coastal lowlands, the southwestern coast, and parts of central Taiwan, respectively.

3.1.5. Main Conclusions

Our roadkill projection models performed well across ecological levels on a national scale. The road-type variable contributed highly to guild-level roadkill risk, indicating that road category strongly influenced roadkill risk. As predictions and variable importance differed across guild and species models, individual models need to be produced for each group of interest. This study demonstrates our predictive roadkill models are scalable to address the ecological question of interest and the importance of systematic collection of roadkill data.

3.2. Introduction

Habitat loss and conversion is the primary cause of biodiversity loss (Brooks et al., 2002; Fahrig, 1997; Gardner, Barlow, & Peres, 2007; Hanski, 2011). The expansion of urban infrastructure, especially roads, is a main driver and facilitator for landscape change (Freitas, Hawbaker, & Metzger, 2010), and has ecological consequences for biodiversity as many roads were built without the ecological knowledge that we have today (Forman & Alexander, 1998). Consequences of roads include the clearly visible direct impacts of wildlife-vehicle collisions (WVCs) (Kroll, 2015; F. Shilling, Perkins, & Collinson, 2015), more commonly referred to as roadkill, and the less-visible, insidious indirect impacts not directly associated with the road. This 'road-effect zone,' the area upon which roads have ecological effects on the surrounding landscape (Forman, 2000), can include a wide range of indirect effects such as changes in soil chemical composition resulting from runoff, barriers and filters to species' movement and any associated reductions in dispersal, and edge effects which can affect species population and community structures (Andrews, Gibbons, Jochimsen, & Mitchell, 2008; Forman & Alexander, 1998). Roadkill and road-effect zones are the unfortunate outcomes of the intersection of human transportation requirements and ecological systems. However, as roads are a necessity for the foreseeable future, we must use data on existing roads and their effects to inform future conservation actions that mitigate biodiversity loss stemming from roads.

Direct and indirect ecological impacts of roads are expected to be especially dramatic in island ecosystems. Despite the high propensity for endemism and high extinction rates, particularly among endemic species (Frankham, 1998), surprisingly little research on the ecological effects of roads has been conducted on islands. Taiwan, an island with high ecological value (Laurance et al., 2014) and high road density (S.-C. Lin, 2006; Phillips, Anderson, Dudík, Schapire, & Blair, 2017) is thus an ideal site for our study. Laurance et al. (2014) concluded that Taiwan's high ecological value outweighs the benefits of building roads in their global road building strategy maps. Taiwan also "appear[s] to feature exceptional … endemism and exceptional threat, but are not sufficiently documented" (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Taiwan already has approximately twice the road density of the U.S.A.: 1.2 km/km^2 and 0.68 km/km^2, respectively (Phillips et al., 2017). This means it is important to study the effects of roads on its ecological structure. Conservation studies of roads in Taiwan stand to offer global application for other developing islands, especially in the highly biodiverse southeast Asian and Pacific regions.

Although roads heavily impact all terrestrial animals, amphibians and reptiles (herpetofauna) have some of the highest levels of recorded road mortality (Andrews, Gibbons, & Jochimsen, 2006; Chyn, Lin, Chen, Chen, & Fitzgerald, 2019), and are the most threatened terrestrial vertebrates in the world (Fitzgerald et al., 2018; IUCN, 2019). Due to their terrestrial lifestyles, diverse life histories, and urgent need for conservation, herpetofauna are ideal for studying road-effect zones across multiple landscape and ecological scales. Previous research has shown road-effect zones can create landscapes near roads that are attractive as reproduction, foraging, or nesting habitat for species, increasing their vulnerability to road mortality (Andrews et al., 2008; Hódar, Pleguezuelos, & Poveda, 2000). Snakes are especially vulnerable to roadkill (Chyn et al., 2019; Farmer & Brooks, 2012), and previous research has shown that environmental variables like proximity to land cover (Gonçalves et al., 2017), foraging guild and body size (Andrews, Gibbons, & Reeder, 2005), and proximity to water bodies (Seo, Thorne, Choi, Kwon, & Park, 2015) may affect snake road mortality.

We collaborated with citizen scientist volunteers to conduct broad, opportunistic roadkill surveys. Our database, the Taiwan Road Observation Network (TaiRON) (Chyn et al., 2019), is a national citizen science project formed in August 2011. The data is opportunistic roadkill data with >60,000 observations collected by >4300 TaiRON citizen scientist members throughout Taiwan, and the data set is continuously growing as the TaiRON citizen science membership is active and increasing. This database is one of the most extensive and complete vertebrate occurrence point data sets in Taiwan, and one of the most extensive roadkill data sets globally (https://globalroadkill.net). Citizen scientists are provided with in-person training, equipment, and a web application accessible across smartphone platforms. Citizen scientists are also encouraged to submit carcasses in good condition to be made into specimens for the Taiwan Endemic Species Research Institute (TESRI) collection. The Taiwan Roadkill Observation Network has garnered proven interest and participation from the public as a thriving government-funded, national citizen science project, and one of the largest roadkill observation systems in the world (Waetjen & Shilling, 2017).

Though roads are widespread and easily accessible, they are often an untapped source of ecological information. One of the most visible and accessible forms of this ecological data is roadkill. Though there is an established literature of localized studies of roadkill patterns (Hobday & Minstrell, 2008; Kioko, Kiffner, Jenkins, & Collinson, 2015; Maschio, Santos-Costa, & Prudente, 2016; Sosa & Schalk, 2016; Taylor & Goldingay, 2004), there is still a paucity of large organized databases of roadkill and large-scale roadkill studies (F. Shilling et al., 2015; van der Ree, Jaeger, van der Grift, &

Clevenger, 2011; Waetjen & Shilling, 2017). To understand and predict WVCs to set conservation priorities, robust, spatially-explicit approaches that take ecological drivers into account are needed to interpret roadkill data.

Reliable modeling of predicted roadkill probability is invaluable to prioritization in mitigation and conservation action towards reducing wildlife-vehicle collisions. Previous research has explored predictive roadkill modeling by analyzing roadkill data with other environmental, and often, anthropogenic variables. Modeling approaches have included mainly regressions (Eberhardt, Mitchell, & Fahrig, 2013; Malo, Suárez, & Diez, 2004; Roger & Ramp, 2009; S. M. Santos, Lourenco, Mira, & Beja, 2013), including MaxEnt (Kantola, Tracy, Baum, Quinn, & Coulson, 2019). Our primary objective was to use TaiRON's large citizen science database of WVC occurrences and the species distribution model (SDM), MaxEnt, to predict the relative probability of roadkill, which we call roadkill risk, for future conservation action. Our study examined the influence of environmental variables on our power to predict the risk of WVCs and herpetofaunal road mortality in Taiwan across several guilds and species. Another aim was to assess the scalability of this approach. As such, we also developed models for a rare snake species with relatively fewer roadkill observations to test the applicability of our predictive roadkill modeling for conservation driven initiatives for vulnerable and rare species. We expected that roadkill risk and environmental variable importance would differ across guilds, species, and other groupings due to differences in life history. Our modeling approach also allowed us to develop a useful conservation and management tool for roadkill mitigation, an intuitive interactive predictive roadkill risk map, for each guild and species of conservation interest. As a 40% increase in global road length is predicted by 2050 (Dulac, 2013), our approach will be invaluable for transportation planning, for example projecting risk of roadkill of proposed roads. This work demonstrates the importance of systematic collection of roadkill data and the utility of our predictive roadkill risk methodology.

3.3. Methods

3.3.1. Study Area

Taiwan is an island roughly 180 kilometers off the eastern coast of mainland China that emerged due to collision of the Philippine Sea plate and the Eurasian plate during the Mio-Pliocene boundary (Adler, HilleRisLambers, & Levine, 2007). As Taiwan is located at the border of the Palearctic and Oriental biogeographic zones and contains elevational heterogeneity, it supports diverse habitats with high biodiversity (He, Gao, Su, Lin, & Jiang, 2018). Taiwan's total area is 36,193 km2 and the climate is subtropical to tropical. The human population of Taiwan is approximately 23 million people with a human population density of 653 people/km2 (Phillips et al., 2017). Taiwan is incredibly biodiverse but also space and resource-limited, making roads and associated removal of habitat more detrimental to faunal populations.

3.3.2. Data

The data were acquired from three sources (Table 1). Data for roadkill occurrences were obtained from the Taiwan Roadkill Observation Network citizen science database, which utilizes social media (Facebook™) and their web application (https://roadkill.tw/app) for data collection and community engagement. Although the data is opportunistic, the database is extensive. Project managers verify individual "unconfirmed" observations for accuracy, which are then either marked as "confirmed" or "unable to confirm." Observations are "confirmed" when consensus is reached on taxonomic identification and locational and date/time data are provided. Data on non-protected species is freely available to the public for live download, whereas protected species and participant data is only available to those who have approved applications. The full TaiRON dataset, including protected species observations, was downloaded on April 24th, 2018, and contained a total of 113,906 observations spanning the years 1995-2018 with the majority of the observations (87%) occurring from 2011 onwards. Data in target taxonomic guilds were then selected (explained below) for analyses.

Table 3.1 Data and data sources.

Data	Data Source
Citizen science roadkill observations	Taiwan Road Observation Network (TaiRON) database (downloaded 24 April 2018)
Road network	GIS-T Transportation Network Geographic Information Storage System: Taiwan Ministry of Transportation and Communication (downloaded 22 November 2017)
Sub-meter land use land cover	GIS-T Transportation Network Geographic Information Storage System: Taiwan National Land Survey and Mapping Center

3.3.2.1. Roadkill Data

For this study we selected three guilds of species, common venomous snakes (CVS), semiaquatic & aquatic snakes (SAS), and turtles, and one rarely observed species, the Maki's keelback snake (*Hebius miyajimae*) (HM), from the TaiRON records based on conservation need and utility for TaiRON projects (Table 2). The semiaquatic and aquatic snake guild (SAS) was chosen due to the high level of threat it faces in

Taiwan. Their habitats are waterways and bodies of water, which are increasingly polluted, modified, or lost, causing major population declines and local extirpations across areas in Taiwan (Chen, Lin, Lin, & Yang, 2017; Mao, 2004). Terrestrial turtles were chosen as turtle populations are also declining in Taiwan, mainly due to illegal poaching for human consumption in Mainland China and habitat loss (Chen et al., 2017; Y.-F. Lin, Wu, Lin, Mao, & Chen, 2010; Zhao, 1998; Zhihua Zhou & Jiang, 2008). The rarely observed Maki's keelback snake, was chosen as it is protected by the Taiwanese government and is an International Union for Conservation of Nature (IUCN) Redlist "vulnerable" species, where roads are listed as a major threat to the species (IUCN, 2019).

We included only TaiRON data containing observations with spatial coordinates and taxonomic identifications that were confirmed by project managers. All roadkill points that were within 30 m of the road network were set to the closest center of a road. This allowed us to account for inaccuracies in GPS location from smart phones. The data partitioned into the following groups: CVS, SAS, turtles, and HM (Table 2).

Table 3.2 Roadkill occurrence groups, the species that comprise the groups, and the number of roadkill occurrences analyzed within each group.

Guild	Species Comprised	Observations
Common venomous snakes (CVS)	*Naja atra, Bungarus multicinctus multicinctus, Protobothrops mucrosquamatus, Deinagkistrodon acutus, Trimeresurus stejnegeri stejnegeri, Daboia siamensis*	4486
Maki's keelback snake (HM)	*Hebius miyajimae*	50
Semiaquatic & aquatic snakes (SAS)	*Amphiesma stolatum, Xenochrophis piscator, Sinonatrix percarinata suriki, Sinonatrix annularis, Myrrophis chinensis, Enhydris plumbea*	1161
Turtles	*Mauremys sinensis, Mauremys mutica mutica, Cuora flavomarginata*	633

Road Network

We cleaned the road network data to contain only roads between 3 m and 100 m in width, as roads narrower or wider likely represented errors. We added a variable-width buffer to road sections that was the width of the section of road, half of the width of the road on each side. For example, a section of road that is 10 m wide will have 5 m of buffer on each side for a total buffer width of 10 m. We converted the road shapefile to a 50 m x 50 m raster (Fig. 3.1A).

3.3.2.2. Environmental Covariates

The Taiwan National Land Survey and Mapping Center provided sub-meter resolution that is classified into 103 land use categories. Many of these categories include specific building-type designations and other categories that would be ecologically irrelevant for our analyses. We reduced the 103 land use categories to 28 environmental covariates by amalgamating repetitive land use types and removing road categories as the data was redundant to the Taiwan Ministry of Transportation and Communication's roadway data. We analyzed 28 environmental covariates for our predictive roadkill risk maps in total (Table 3), with the covariate "road type" as a categorical variable (Table 4). We excluded elevation because it is often highly correlated with other environmental variables and has low contribution to models (Bradie & Leung, 2017).

We conducted pre-model fitting covariate selection by testing for correlations between our variables. None of the correlations were over the moderate correlation value of 0.5 for the 28 variables, so all variables were kept in the model. Additionally, all non-categorical variables were standardized to aid in model fitting and result interpretation.

After choosing our environmental covariates, we converted the polygon shapefiles to 50 m x 50 m rasters for each covariate. We calculated percentage cover to capture the spatial effect of land use category covariates up to 250 m outside of its delineated area. A 250 m x 250 m moving window was chosen because ecological studies on snakes and turtles in Taiwan and other tropical climates report home ranges generally within 62500 m2 (or 250 m x 250 m) (Brown, Shine, & Madsen, 2005; Lue & Chen, 1999; Rodda, Fritts, McCoid, & Campbell III, 1999). We used the “focal” function in the raster R package to create percent cover layers. For covariates relating to waterways or bodies of water, we calculated Euclidean distance (Fig. 3.1B), as these water features are generally attractive to fauna and distance to water may have ecological spatial effects (Farmer & Brooks, 2012; Langen, Ogden, & Schwarting, 2009). We created Euclidean distance-to-variable gradients for these environmental variables using the “Proximity (raster distance)” tool in QGIS (Fig. 3.1B). We masked all of the covariate gradients to the rasterized Taiwan road network (Fig. 3.1D). This is to constrain the roadkill model to areas where fauna-vehicle interactions are expected.

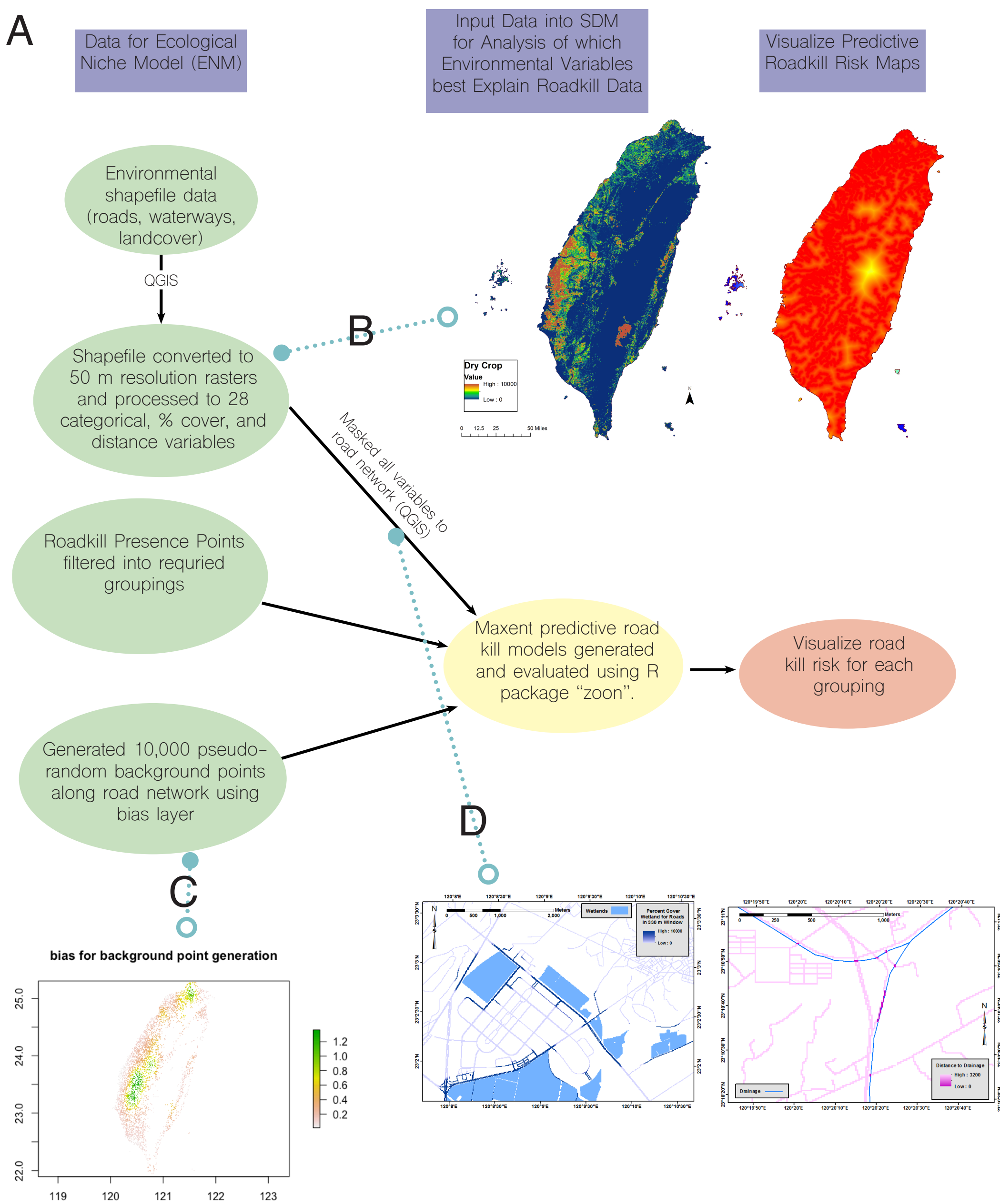

Figure 3.1 Flowchart of predictive roadkill risk model methodology. A) Flowchart of data processing methodology and statistical analysis with three main sections, data, analysis, and visualization. B) Examples of unmasked % cover and distance environmental variables (Dry Crop and River variables, respectively). C) Bias layer for generating pseudo-random background point. D) Zoomed in sections of masked environmental variables (wetland % cover, distance to drain).

Table 3.3 Environmental covariate names and definitions.

Environmental covariate	Definition
Road type	Type of road defined by the Taiwan Ministry of Transportation and Communication. This is a categorical variable. See Table xx for road categories
Road width	Width of roads in meters.Roads analyzed are 3 m ≤ and ≤ 100 m.
Land Usage Percent Cover (w/ 250 m window)	
Buildings	Buildings are permanent structures with a roof and walls
Dry field crop	Agricultural field crops that are grown on dry land
Fruit trees	Agricultural fruit tree orchards
Grassland	Grassland
Harvested forest	Harvested forest without regrowth
Managed bamboo	Managed bamboo forest (> 75% bamboo)
Managed broadleaf	Managed broadleaf forest (> 75% broadleaf)
Managed conifer	Managed conifer forest (> 75% conifer)
Managed mixed forest	Managed mixed forest
Mining	Mining activities, including rock quarries and salt mines
Parks	Recreational parks
Pasture	Agricultural livestock pastures
Rice	Agricultural rice
Shrub land	Shrub land
Virgin bamboo	Virgin bamboo forest (> 75% bamboo)
Virgin broadleaf	Virgin broadleaf forest (> 75% broadleaf)
Virgin conifers	Virgin conifer forest (> 75% conifer)
Virgin mixed forest	Virgin mixed forest
Wasteland	Agricultural fields that have been exhausted
Distance to variable	
Aquaculture	An artificial body of water for farming fish
Beaches	A landform alongside a body of water typically consisting of loose particles of rock
Beach wetland	An area of land on or alongside a beach inundated with marine water
Cistern	An artificial reservoir for storing water
Ditch	An artificial small to moderate depression created to channel water
Riverways	A naturally-formed waterway that is rendered as a line
Wetlands	An area of inundated land

Table 3.4 Road categories

Number	Road code	Road type
1	1E	Provincial highway fast road
2	1U	Provincial highway collinear
3	1W	Provincial highway
4	2U	County road collinear
5	2W	County road
6	3U	Township (country) road collinear
7	3W	Township (country) road
8	4W	Industrial road
9	AL	Urban roads (Lane, Alley)
10	FR	N/A
11	HU	National (state) Highway subsidiary road
12	HW	National (state) Highway
13	OR	With (having) road name but cannot be classified
14	OT	No road name
15	RD	Urban roads (Road, Street)
16	RE	Urban fast road

3.3.3. Analysis

We related observed roadkill records to environmental covariates to predict roadkill distributions, or "roadkill risk," across a road network. We employed SDMs rather than popular hotspot and clustering analyses for roadkill analyses (F. M. Shilling & Waetjen, 2015) as we believe SDMs to have several advantages. Species distribution models can both predict relative roadkill rates in areas without roadkill observations and can identify the variables that best explain presence of roadkill, whereas hotspot and cluster analyses can only highlight spatially clustered data and cannot predict into unsampled areas as they do not incorporate environmental or landscape variables. Previous studies have used various predictive models for analysis on roadkill (Gomes, Grilo, Silva, & Mira, 2008; Malo et al., 2004; Ramp, Caldwell, Edwards, Warton, & Croft, 2005), but few studies have employed MaxEnt for vertebrate road mortality

(Garrote, López, López, Ruiz, & Simón, 2018; Ha & Shilling, 2017; Kantola et al., 2019; Y.-P. Lin et al., 2019). We provide novel use of MaxEnt to predict roadkill mortality across a road network utilizing our large and robust citizen science database.

We chose to use the MaxEnt modeling method (Phillips, 2005), one of the most widely used SDMs (Elith et al. 2011), for our predictions as it can be applied to presence-only datasets and incorporates regularization to reduce overfitting, which facilitates the use of a large number of covariates (Merow, Smith, & Silander, 2013). This is important because the TaiRON roadkill data consists only of opportunistic observation records, so it is presence-only data. We used the R package 'zoon' (v0.6.3) (Golding et al., 2017) to create a reproducible workflow for our SDM analyses. MaxEnt uses maximum entropy estimation to fit a model to data (for details, see Merow et al., 2013). We employed all available MaxEnt feature types (linear, quadratic, hinge, threshold, and product) as more than 80 presence points were available for each group (Merow et al., 2013) except HM, however, we wanted to keep methodology consistent across models. MaxEnt is a presence-background modeling method, so we generated 10,000 background points using a bias layer to account for sampling bias (Dudík, Phillips, & Schapire, 2006; Phillips et al., 2009). Our bias layer was created using a two-dimensional kernel density estimate based on the coordinates of the presence points. This was then masked to the road network (Fig. 1C). This means that our background samples are biased towards areas with a higher density of occurrence points and background points would be generated with the same biases inherent in the occurrence data. Generating biased background points assures the same environmental biases in both presence and background data and the model will account for sampling bias (Dudík et al., 2006; Phillips et al., 2009). We utilized biased background sampling because sampling effort could not be estimated across our landscape as the nature of roadkill confounds the state and observation processes, and we had data on roadkill occurrences of other taxa that employed the same sampling methods (Merow et al., 2013). Following TaiRON protocol, roadkill observations were removed from the road once recorded, which removes the risk of multiple observations of the same individual due to higher sampling effort. We also selected additional options for jackknife and variable percent contribution analyses as measures of variable importance. We turned off "auto features" so that MaxEnt would include all model features instead of just one to ensure consistent methodology across models.

3.3.4. Model Evaluation

We ran 10-fold cross-validation (k = 10) in all models and used the Area Under the Receiver Operating Characteristic Curve (AUC) model evaluation metric to help assess the performance of our model. We provide the test AUC, training AUC as well as the overfitting statistics of AUC difference (AUCdiff = training AUC – test AUC) (Warren & Seifert, 2011) and minimum and 10th percentile training presence threshold omission rates (Radosavljevic, Anderson, & Araújo, 2014) to test for overfitting. Cross-validation is especially helpful for SDMs when there is no independent dataset available to validate model predictions. In our analysis, the data was split into 10 dataset folds, and we fit a model to every possible combination of 9 folds, known as the training dataset, and then evaluated the model's predictions on the remaining hold-out fold, known as the testing data (see Appendix A). The continuous projections of the 10 MaxEnt training set models were combined by averaging to create a training set ensemble (TSE) model. Additionally, as *H. miyajimae* had a relatively small sample size (n = 50), we employed a hold-one-out jackknife approach, where during cross-validation, k is equal to the number of presences to maximize the utility of information from species with few records (k = n = 50) (Shcheglovitova & Anderson, 2013). Consequently, we developed MaxEnt TSEs of both 10 and 50 models for *H. miyajimae*. The AUC was used as a metric to evaluate performance for all models when data was cross-validated as it is a threshold-independent metric that can be used for presence-only models. We chose to report variable importance as a measure of permutation importance rather than percent contribution, as permutation importance has been shown to be a more accurate and reliable predictor for variable selection accuracy (Halvorsen, 2013; Searcy & Shaffer, 2016).

For all above analyses, we used the following programs and R packages: R 3.5.1 (Team, 2017), QGIS 2.18.14 (QGIS Development Team , 2019), MaxEnt 3.4.1 (Steven J. Phillips, Miroslav Dudík, & Schapire, 2017), 'zoon' (Golding et al., 2017), dismo (Robert J. Hijmans, Steven Phillips, John Leathwick, & Elith, 2017), and 'caret (Max Kuhn. Contributions from Jed Wing, Engelhardt, & Lescarbeau, 2018).

3.4. Results

We produced predictive roadkill risk maps for the aforementioned groups (CVS, SAS, turtles, and HM) (Fig. 2-6). We also produced interactive versions of these predictive maps, which allow users to zoom in on details of the predictive model (see

Appendix A). Each respective group produced differing predictions of roadkill risk across Taiwan's road network, and several environmental variables best explained the presence of roadkill for each guild.

The predictive maps for CVS showed patterns of higher risk of road mortality were widespread across Taiwan's rural inner montane regions, with some of the highest mortality on trans-national highways that cut through the steep and rugged central mountain range (Fig. 2). The following covariates had the highest permutation importance: road type, buildings, road width, virgin mixed forest, and rice (Table 5, see Appendix A). The model had the following performance metrics: test AUC = 0.717, training AUC = 0.734, and the AUC_{diff} = 0.017. The minimum training presence threshold omission rate = 0.000, and the 10^{th} percentile training presence threshold omission rate = 0.100.

The predictive maps for SAS show patterns of higher risk of road mortality that are widespread along coastal lowlands of Taiwan, and low risk of road mortality is concentrated in the steep, high-elevation, rugged central mountain range (Fig.3). The following covariates had the highest permutation importance: road type, ditch, road width, buildings, beach wetland (Table 5, see Appendix A). The model had the following performance metrics: test AUC = 0.772, training AUC = 0.797, and the AUC_{diff} = 0.025. The minimum training presence threshold omission rate = 0.000, and the 10^{th} percentile training presence threshold omission rate = 0.100.

The predictive maps for turtles show patterns of higher risk of road mortality concentrated on the southwestern coast in Taiwan, mostly in Chiayi and Tainan counties

(Fig. 4). The following covariates had the highest permutation importance: road type, buildings, rice, road width, fruit trees (Table 5, see Appendix A). The model had the following performance metrics: test AUC = 0.798, training AUC = 0.832, and the AUC_{diff} = 0.034. The minimum training presence threshold omission rate = 0.000, and the 10^{th} percentile training presence threshold omission rate = 0.100.

Under the k = 10, k-fold cross-validation model, the predictive maps for HM show patterns of higher risk of road mortality concentrated in a few regions in central Taiwan (Fig. 5). The following covariates had the highest permutation importance: managed bamboo forest, fruit trees, cistern, beach wetland, and road width (Table 5, see Appendix A). The model had the following performance metrics: test AUC = 0.982, training AUC = 0.998, and the AUC_{diff} = 0.016. The minimum training presence threshold omission rate = 0.000, and the 10^{th} percentile training presence threshold omission rate = 0.081.

Under the k = n (= 50), k-fold cross-validation model, the predictive maps for HM show patterns of higher risk of road mortality similarly concentrated in a few regions in central Taiwan as in the k = 10 model (Fig. 6). The following covariates had the highest permutation importance: managed bamboo forest, buildings, fruit trees, beach wetlands, and riverways (Table 5, see Appendix A). The model had the following performance metrics: test AUC = 0.980, training AUC = 0.997, and the AUC_{diff} = 0.017. The minimum training presence threshold omission rate = 0.000, and the 10^{th} percentile training presence threshold omission rate = 0.081.

Both HM models with (k =10) and (k = n = 50) produced similar predicted roadkill risk maps (Fig. 5, 6) and had similar model performance. Our overfitting statistic, AUC_{diff}, for the HM (k = 10) and HM (k = n) models were comparatively low, suggesting overfitting was not a problem. Additionally, the minimum and 10^{th} percentile training presence omission rates were not higher than the theoretical expectation for the thresholds, 0% and 10 %, respectively, and do not indicate overfitting for either HM model. Due to a small sample size, the AUC may be inflated due to modeling a small number of mostly clustered occurrences over a large area, which gives a largely dichotomous relative probability estimate.

The models produced for the three guilds, CVS, SAS, and turtles performed well, with all models holding AUCs > 0.77. The road type variable had the highest permutation importance across all three guilds. This is likely because we are predicting onto the road network itself, so the variable will correlate strongly with the road variables. As road type is a categorical variable, the types of roads that most strongly influenced roadkill probability for CVS, SAS, and turtles were types 1W (provincial highways), 2U (two-lane county roads), and 2U (two-lane county roads), respectively. The protected species model, HM, had a very high AUC, and the low overfitting statistic compared to the models for various guilds suggests the elevated AUC metric is not due to overfitting. However, the high AUC may also be due to a small sample size modeled over a large area.

Clear spatial associations between environmental variables and road mortality of herpetofaunal taxa were revealed in the MaxEnt roadkill risk models. Overall, the environmental variables with the highest permutation importance to road mortality points across taxa were related to characteristics of roads. Response curves for the top five contributing variables for each group showed how strongly each environmental variable affected the model predictions and are given in Appendix A.

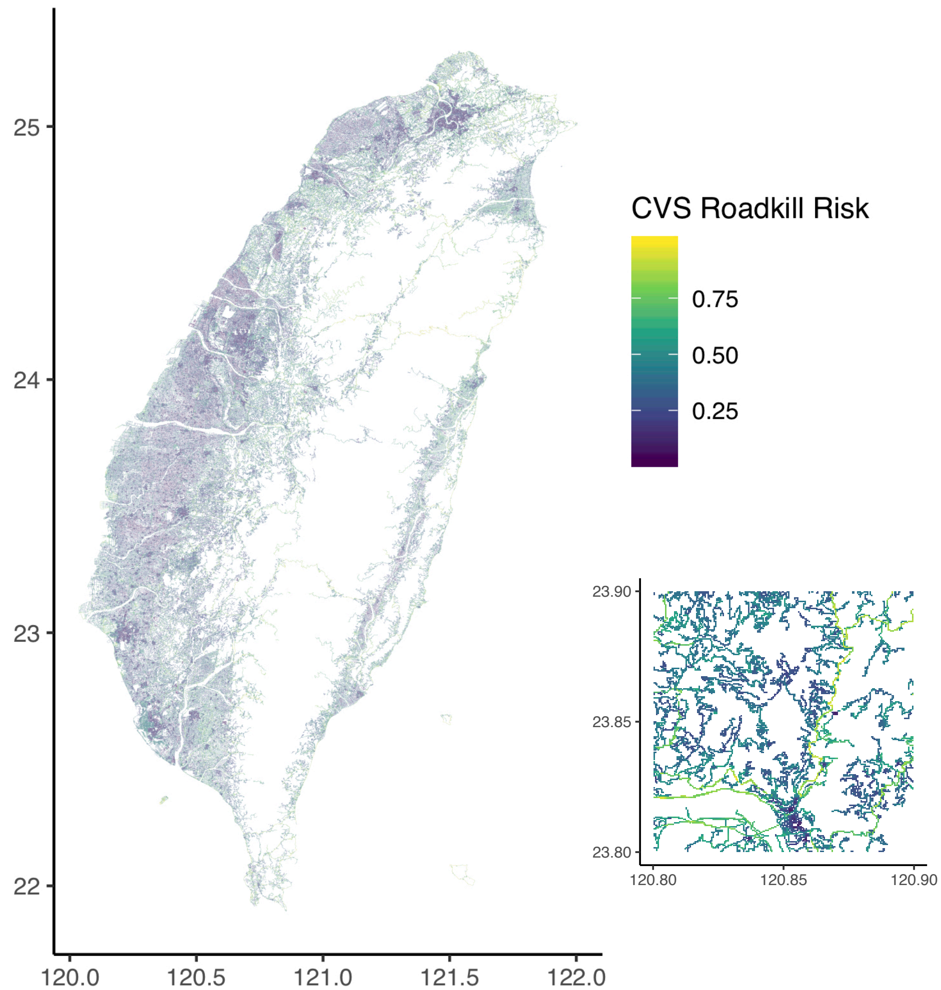

Figure 3.2 The predicted roadkill probability ("risk") for common venomous snakes (CVS) in Taiwan with an inset at the bottom right to show detail. Values closer to 1 (yellow) denote higher risk of roadkill and values closer to 0 (purple) denote lower risk

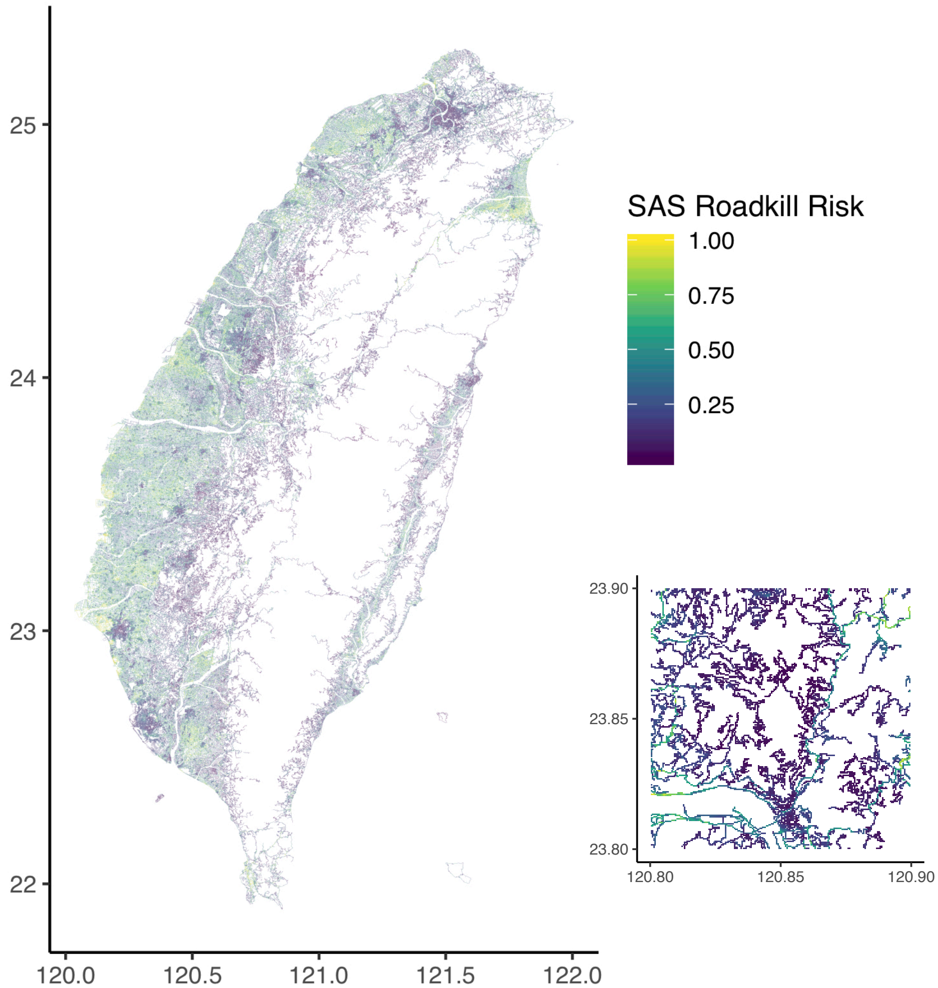

Figure 3.3 The predicted roadkill probability ("risk") for semiaquatic & aquatic snakes (SAS) in Taiwan with an inset at the bottom right to show detail. Values closer to 1 (yellow) denote higher risk of roadkill and values closer to 0 (purple) denote lower risk

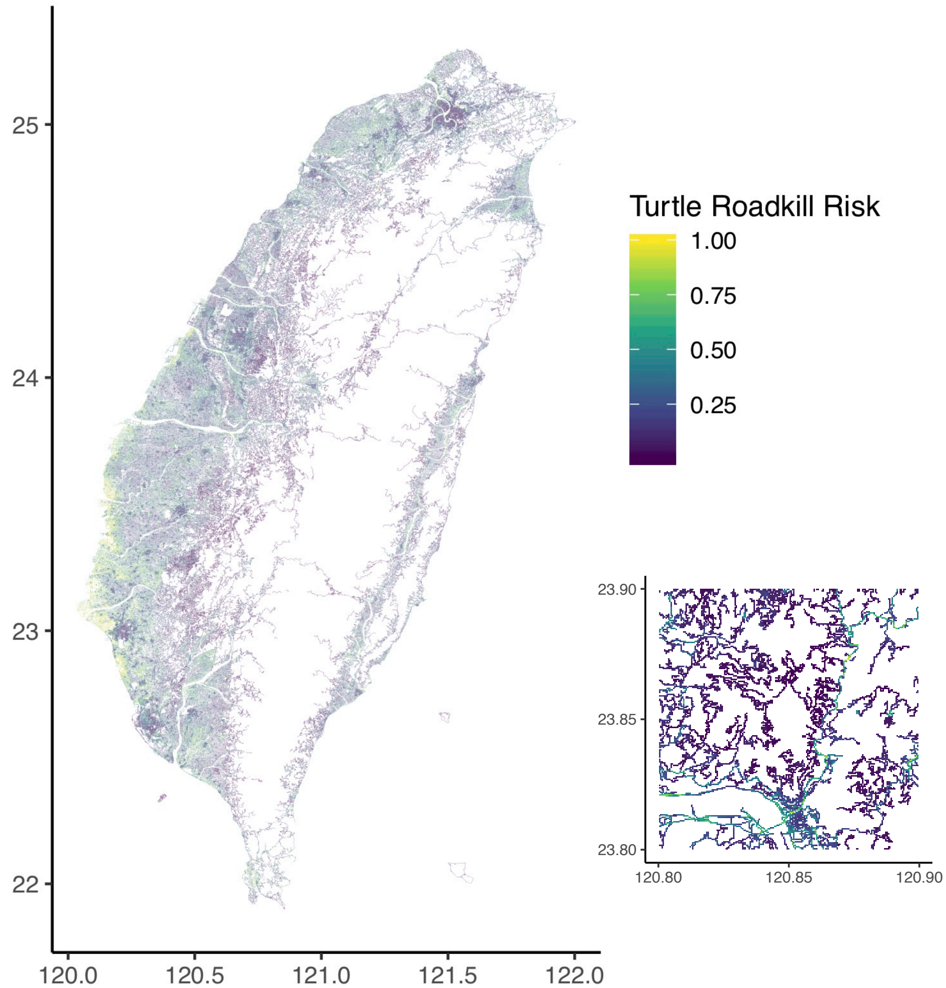

Figure 3.4 The predicted roadkill probability ("risk") for turtles in Taiwan with an inset at the bottom right to show detail. Values closer to 1 (yellow) denote higher risk of roadkill and values closer to 0 (purple) denote lower risk.

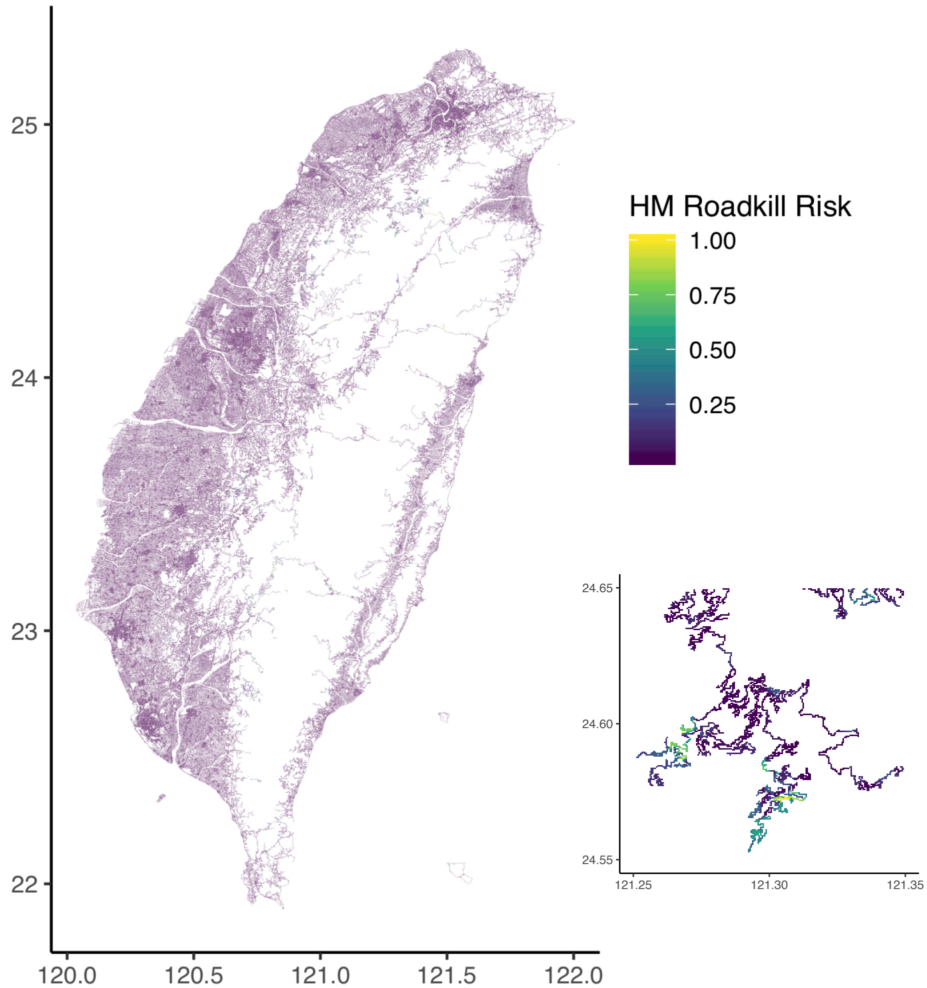

Figure 3.5 The predicted roadkill probability ("risk") for *Hebius miyajimae* (HM) in Taiwan using k = 10 fold cross-validation with an inset at the bottom right to show detail. Values closer to 1 (yellow) denote higher risk of roadkill and values closer to 0 (purple) denote lower risk.

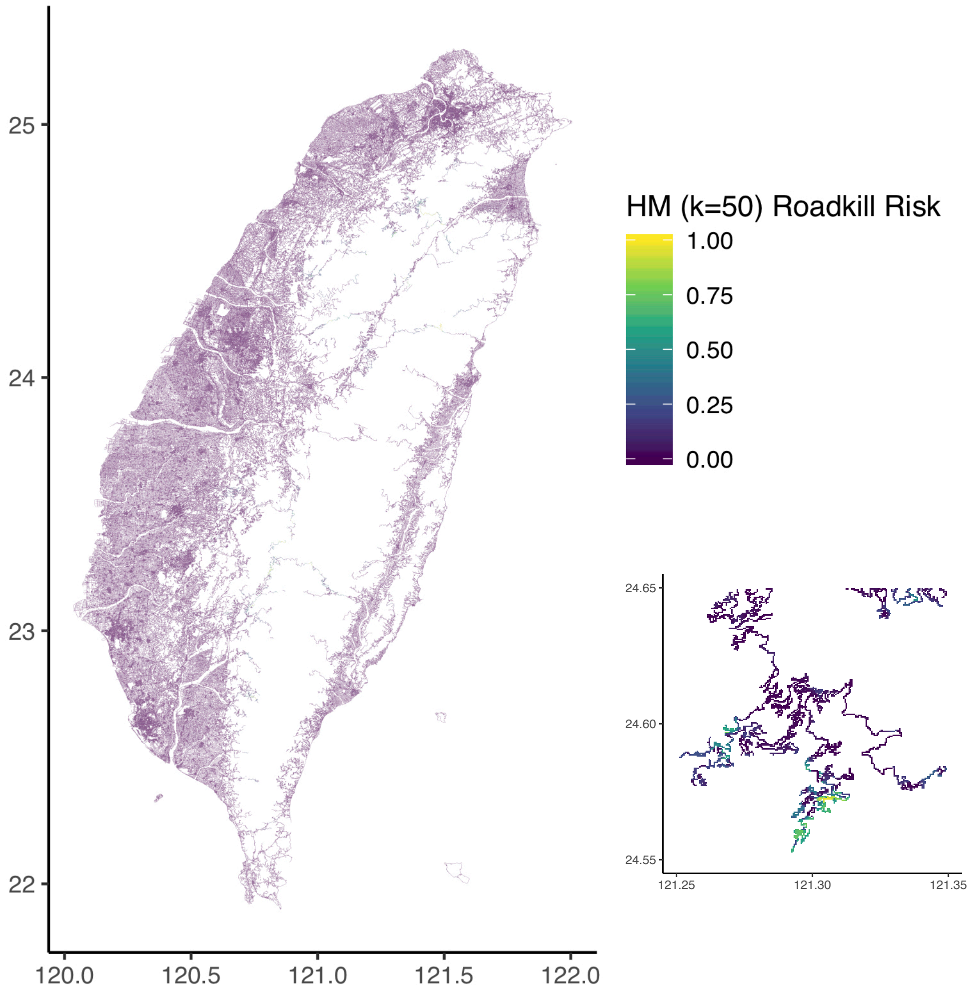

Figure 3.6 The predicted roadkill probability ("risk") for *Hebius miyajimae* (HM) in Taiwan using k = n (= 50) fold cross-validation with an inset at the bottom right to show detail. Values closer to 1 (yellow) denote higher risk of roadkill and values closer to 0 (purple) denote lower risk.

Table 3.5 Variable importance measurements for each model where PC = percent contribution and PP = permutation importance

covariate	CVS[1]		SAS[2]		Turtles		HM[3](k = 10)		HM[3](k = n)	
	PC	PP	PC	PP	PC	PP	PC	PP	PC	PP
aquaculture	0.2	0.8	9.3	4.5	19.5	6.4	3.9	0.4	0.7	0
beaches	0.7	1.2	1.4	6	0.6	1.4	1.7	0.2	3.9	3.5
beachwetland	0.3	0.3	2.1	6.4	1.6	5	3.5	2.1	2.8	7.3
buildings	19.1	15.2	5.7	8.4	5.4	16.3	1.2	0.5	1	15
cistern	1	1.1	6.9	4.5	2.6	0.4	39.7	4.2	38.7	3.4
ditch	0	0	14.2	11	5	4.2	0.2	0	0.4	1.1
dry field crop	0.4	1.7	0.5	1.6	1	2	0.4	0.3	0.1	0.5
fruit trees	0.6	8.1	0.8	4	1.7	7.1	0.8	13.6	0.7	11.8
grassland	0.3	0.2	0	0.1	0.1	0.2	0	0	0	0
harvested forest	0	0	0	0	0	0.2	0	0	0	0
managed bamboo	0	0	0.2	0.3	0.7	1.9	0.5	74.6	0.6	35
managed broadleaf	0.3	0.1	0.4	1.9	2.4	2.2	0.4	0.7	0.3	0.5
managed conifer	0	0	0.3	0.6	0	0.2	0.3	0.2	0.1	0.4
managed mixed forest	2.9	3.8	0.5	4.2	0.7	4.9	1.7	0	1.3	0.2
mining	0	0	0.1	0.1	0.1	0	0	0	0	0
parks	0	0	0	0	0.7	0.6	0	0	0	0
pasture	0	0	0	0	0	0	0	0	0	0
rice	4.7	8.8	8.3	3.9	1.2	8.5	0.1	0.3	0.1	1.4
riverways	1.2	1.5	3.3	6.1	3.3	5.9	0.4	0.3	1.2	6.9
road type	35.8	26.7	17.8	19.6	17.9	17	35.4	0.7	36.5	6.2
road width	18.9	11.9	21.3	8.8	25.1	7.5	1.7	1.2	1.4	5.3
shrubland	2.4	2.4	0.1	0	0	0	0	0	0	0
virgin bamboo	0.1	0	0	0.1	0	0	0	0.1	0	0
virgin broadleaf	0.4	0.9	0	0.1	0.2	1.6	0.1	0	0.1	0
virgin conifers	0	0	0.1	0.1	0	0	0	0	0.1	0
virgin mixed forest	8.9	10.6	0.6	1.9	0.5	3.1	7.9	0.4	9.7	1.6
wasteland	0	0.1	0.4	0.2	1.7	1.2	0	0	0	0
wetlands	1.7	4.6	5.6	5.7	7.7	2.1	0.2	0.3	0.1	0.1

[1] Common Venomous Snakes
[2] Semiaquatic & Aquatic Snakes
[3] *Hebius miyajimae*

3.5. Discussion

We modeled roadkill risk across several taxonomic scales (i.e., guilds and species), and our methods and associated maps revealed versatile options in applicability. A meaningful contribution of this paper is demonstration that the predictive modeling approach we employed can easily be scaled up or down, depending on the ecological question. The methodology is globally applicable anywhere there is sufficient roadkill data. This work also highlights the utility and importance of amassing roadkill data, as it can greatly contribute to both informing future conservation action and engaging the public in wildlife education and conservation ethics. Specifically, we made novel findings on where predicted high and low risk areas are for threatened guilds of reptiles in Taiwan and identified which environmental variables, including variables about the roads themselves, contributed most to high roadkill predictions. Additionally, the interactive roadkill risk map can be a useful conservation tool for managers. To our knowledge, this study is the first to utilize an SDM and a roadkill database to predict roadkill presence, or "risk," directly to a road network on a national scale. Importantly, this methodology and its findings are not limited to Taiwan; it can be applied to any area with sufficient roadkill and environmental data.

Lin et al., (2019) recently used TaiRON data to separately model annual and seasonal roadkill of four common herpetofaunal species in Taiwan at 1 km resolution. They followed a framework that used the SDM of habitat as the only environmental correlate of exposure with road characteristics as environmental correlates of hazard to develop a model with roadkill data as response variable input (Visintin, Ree, & McCarthy, 2016). Our study followed the more traditional approach using raw environmental correlates (e.g., land cover variables as opposed to solely a habitat model) with road characteristics to model roadkill risk (e.g., Ha & Shilling, 2017; Kantola et al., 2019). In addition, we utilized finer 50 m resolution that is more suitable for the scale of road characteristics. Our use of raw environmental correlates allowed representation of individual correlates as both elements of exposure (habitat suitability) and risk. For example, the land cover of ditches may have an intermediate habitat suitability value of exposure for a semiaquatic species and may also represent a high value of risk around roads due to use as corridors for movement. Further use of our approach with seasonal data, as done by Lin et al. (2019), should be explored.

Our models predicted relative probabilities of roadkill and serve to identify key sections of the road network with high predicted risk of roadkill for further investigation or mitigation. Examining these key areas and environmental variables associated with WVCs and wildlife mortality would allow managers to plan to avoid and mitigate these deadly encounters, which is especially important for rare and protected species (Chyn et al., 2019). Road mitigation measures are a crucial component in Taiwan's transportation management due to the intersection of their extensive density of roads and high wildlife biodiversity and endemism. Translating our models into an interactive mapping tool helps make our results immediately applicable to management of WVCs in Taiwan at the national level.

Importantly, our study demonstrates the utility of using SDMs to predict roadkill risk for endangered species based on relatively few observations. *Hebius miyajimae* is a forest-dwelling species restricted to relatively undisturbed forests in Taiwan of high conservation priority (Z. Zhou, Lau, Jiang, & Lin, 2016). Both models (k = 10 and k = n = 50) produced near identical predictive maps and model performance metrics. The similarity of the k = n with the k = 10 model outcomes suggest that the k = 10 model utilized sufficient information with a small sample size. The high AUCs and limited high roadkill risk areas in both models were likely due to strong association between environmental covariates and habitat of this specialist species. Thus, model predictions were likely not overfitted as the areas with highest predicted risk coincided with more heavily forested and less developed regions of Taiwan's central mountain range with only three highways that cross the range and island. Expectedly, the transnational provincial highway road types were identified as the road type with the highest correlation to *H. miyajimae* roadkill. Interestingly, the strong prediction that managed bamboo forest was inversely correlated with HM roadkill risk may be due to the high amount of disturbance managed bamboo forests receive from consistent harvesting and a lack of forest diversity (see Supporting Information Appendix S3.4-S3.5). Modified habitats with strongly negatively correlated variables were the highest contributing factors behind HM roadkill risk. This broader model is an important first step for identifying major areas for conservation and top variables that contribute to roadkill risk of *H. miyajimae*. However, MaxEnt provides relative suitability predictions, so the isolated model predictions of high roadkill risk areas in both HM models may also be due to analysis with few clustered roadkill occurrences over a large area. A finer-scale study of HM roadkill risk modeling is recommended to more specifically isolate and identify habitat variables contributing to HM roadkill risk in a smaller area.

The road-type variable contributed highly to guild-level roadkill risk, which means that the category of road likely strongly influenced the risk for roadkill of these guilds. Provincial highway type was most correlated with CVS roadkill. Higher roadkill risks may exist on provincial highways for CVS, as these highways tend to carry a larger volume of traffic than smaller country roads, but they also run through less developed regions that are surrounded by more potential CVS habitat. The importance of low building cover and high virgin mixed forest cover in CVS roadkill projections is indicative of expected CVS habitat preferences. In contrast, although SAS roadkill projections were also associated with low building cover, they were also associated with higher cover of wetland habitats preferred by SAS, such as ditches and beach wetland. County road collinear type, areas are where two roads merge, most highly contributed to both SAS and turtle guild roadkill risk. Colinear roads may contribute more to roadkill risk of SAS and turtle guilds because traffic from two or more roads is funneled into one, creating a higher probability of WVCs at these locations (see Supporting Information Appendix S4). These findings can help transportation managers prioritize mitigation strategies for colinear roads.

Potential concerns for using SDMs for modeling roadkill risk for larger taxonomic or functional groupings is that model suitability may be noisier as there are potentially drastically different ecological niches for species within the same groupings. Although the strength of our model predictions was potentially affected by this variation in life histories and habitat preferences among species within the guilds, the AUCs for each guild were high (>0.77), indicating the models performed well (Lobo, Jiménez-Valverde, & Real, 2008). For example, both arboreal and terrestrial snakes were included in the CVS guild, though the species of snakes have different habitat associations (e.g. forest and grassland). Another concern with SDMs in general is modeling with too few data, which is often the case for rare or endangered species, as the model may be prone to overfitting. However, modeling as guilds, or other higher-order groupings, allows sharing of information between common species and those with few observations. Summarizing, our models based on a priori assignment of species into ecological guilds were successful in producing useful predictive roadkill maps with good performance across ecological levels on a national scale.

The scalability of our approach proved useful to reveal impacts of roads on wildlife across multiple ecological scales. At the species level, our models showed that restricted species might be further confined to smaller habitat patches, which may be the case with the HM model. The HM model did not predict much roadkill across Taiwan's road network but predicted high risk on roads in areas with lower road density. These roads have the potential to cause further isolation of *H. miyajimae* populations in these regions that our models have identified as it has been shown that genetic isolation of wildlife populations can be caused by roads (Holderegger & Di Giulio, 2010) through barriers of movement (Andrews et al., 2005; Robson & Blouin-Demers, 2013) and genetic isolation in snakes (Clark, Brown, Stechert, & Zamudio, 2010). At higher ecological scales, models may elucidate patterns of impact on functional guilds or larger taxonomic groups. For example, though CVS and SAS are both guilds of snakes, the areas identified as high roadkill risk were almost reversed across the island. Common venomous snakes had high roadkill risk in rural montane regions of Taiwan, whereas SAS risk was highest in coastal lowlands. Thus, this study indicates both the ecological scalability of our approach as well as the need for individual roadkill risk models for each taxonomic grouping of interest. High and low roadkill risk varied greatly across models, even in guilds within the same suborder (Serpentes, i.e. CVS and SAS). These ecologically meaningful guilds had vastly different patterns of roadkill risk (Figs. 2-6) across the island and would need targeted mitigation efforts that vary according to identified environmental factors of high roadkill risk contribution and areas of high risk.

We recognize limitations of opportunistic roadkill data. Variability in detection of roadkill may occur, which may introduce spatial, taxonomic, or temporal bias. Opportunistic datasets are incomplete and do not accurately identify all areas with roadkill risk, so predicting roadkill probability in areas without observations is especially valuable. We accounted for these potential issues by using biased background points in the models. Datasets on effort to collect roadkill data would allow further enhancement of predictive roadkill models, however, like most other roadkill databases, TaiRON does not quantify sampling effort. Additionally, roadkill often goes unnoticed for a variety of reasons (S M Santos, Carvalho, & Mira, 2011; Skórka, 2016). Our models are meritorious as a tool for identifying locations where actionable conservation mitigation and further research can occur in Taiwan. These roadkill risk models can provide important predictions that supplement and compensate for lacking data.

Our findings highlight the utility of predictive roadkill modeling as a tenable conservation product for conservation practitioners. Once key roadkill variables are identified, roadway and landscape management and mitigation can reduce the impact of these variables on roadkill risk. Possible mitigation measures include enhancing habitat connectivity (wildlife crossing structures, culverts, etc.), fencing, seasonal traffic reduction (i.e. breeding season), and reducing traffic speed and can be prioritized for areas identified as high roadkill risk. Future research should be targeted at ground-truthing validation of these roadkill risk models, comparing outputs and accuracy of models created with different SDMs, and testing the methods we describe in different regions. We also suggest incorporating finer resolution micro-habitat variables for habitat specialists as these variables could identify key fine-scale landscape characteristics that contribute to roadkill risk. We hope our predictive roadkill risk models will contribute to informing current and future transportation mitigation and planning globally

3.6. References

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4. ROADS ARE HELL FOR THE DEVIL: PREDICTIVE ROADKILL RISK MODELING FOR THE TASMANIAN DEVIL (SARCOPHILIUS HARRISII)

4.1. Synopsis

In recent decades, the Tasmanian devil (*Sarcophilus harrisii*) has seen an over 85% decrease in overall population due to devil facial tumor disease (DTFD). These depleted devil populations are at increasingly higher risk of local extirpation from other added threats to survival. One major cause of mortality is wildlife-vehicle collisions (WVCs). Additionally, many devil behaviors and traits compound risk of WVC, such as foraging and traveling along roads, nocturnal activity, their dark black pelage, and tendency to roam large distances. Due to the threat of WVCs to devil survival, our primary objective was to use the species distribution model (SDM) MaxEnt and devil roadkill records to predict the relative probability of roadkill across the Tasmanian road network, or roadkill risk. We aim to describe the spatial patterns of devil roadkill in Tasmania, identify environmental and anthropogenic variables that contribute to roadkill risk, and develop a predictive roadkill risk tool to help conservation and transportation managers mitigate or prevent devil mortality on roads. We provided novel use of MaxEnt to predict roadkill mortality for devils across the Tasmanian road network utilizing citizen science roadkill observations. The results will be used to inform transportation management and to make recommendations to reduce the ecological impacts of roads on Tasmanian devils.

4.2. Introduction

The world's largest surviving marsupial carnivore has seen rapid population declines across its endemic range for the past two decades. Devil facial tumor disease (DFTD), an infectious disease affecting Tasmanian devils (*Sarcophilus harrisii*) with almost 100% adult mortality, has led to an overall population decrease of over 85%, with local declines of over 90% (Hendricks et al., 2017; Lazenby et al., 2018; McCallum et al., 2009). The disease was first discovered in northeastern Tasmania in 1996 and has since spread over 95% of the species' geographic range (Storfer et al., 2018). Moreover, depleted devil populations are at increasingly higher risk of local extirpation from other threats that were not previously considered significant. Under normal circumstances, threats such as secondary poisoning, illegal persecution, and competition from feral animals (e.g. foxes) would probably not greatly increase risk of endangerment (Brüniche-Olsen, Jones, Austin, Burridge, & Holland, 2014; Lawrence & Wiersma, 2019; McCallum & Jones, 2006; Rose, Pemberton, Mooney, & Jones, 2017). In particular, the threat that potentially has a more significant and detrimental impact on depleted Tasmanian devil populations is road mortality from wildlife-vehicle collisions (WVCs) (Lawrence & Wiersma, 2019).

Significant conservation efforts have been made to maintain functional devil populations in the wild, including the establishment of captive breeding programs (McCallum & Jones, 2006, 2010) and wild DFTD-free populations (C. Grueber, Peel, Wright, Hogg, & Belov, 2019), vaccine development (Kreiss, Brown, Tovar, Lyons, & Woods, 2015), and augmentation of wild populations (Fox & Seddon, 2019). Early attempts to augment or re-establish wild devil populations with captive-bred devils were hampered by high WVC mortality following release (C. E. Grueber et al., 2017) as genetic and behavioral adaptation to the captive-environment over successive generations may have left captive-born devils to be naïve to the threats associated with roads (Rabin, 2003). Instead, wild disease-free populations are managed in isolated locations such as Maria Island and Forestier Peninsula, and individuals are taken from these populations as propagules for translocations to enhance the stock population and improve genetic diversity. Although wild-bred devils are less vulnerable to WVCs than captive-bred devils following release, roadkill can still potentially limit the success of important conservation activities if not locally managed. As WVCs are an important source of devil mortality, understanding the risk of roads on devils is important for Tasmanian devil conservation.

Several aspects of Tasmanian devil life history may also compound WVC risks. Devils are wide-ranging carnivorous mammals with an average overlapping home range of 13.3 km^2 and a neighborhood size of about 100 km (Rose et al., 2017). Thus, individuals tend to roam large distances across the landscape and may encounter many roads per day. Extensive gene flow has been found which suggests that distances moved are large (Jones, Paetkau, Geffen, & Moritz, 2004). Devils also travel and forage along habitat edges and anthropogenic linear features, such as roads, as these corridors facilitate rapid travel and provide opportunities for hunting and scavenging (Andersen, Johnson, Barmuta, & Jones, 2017; Frey & Conover, 2006). Carnivores with large home ranges and dispersal distances are particularly vulnerable to the effects of roads and road network expansion (Grilo, Smith, & Klar, 2015). Jones et al. (2004) identified two major genetic subpopulations of devils, one on the eastern half of Tasmania and the other on the northwestern corner (near Marrawah). A band of unsuitable habitat including farmland, cleared land, urban development, steep rocky areas, dense wet forest (e.g. rainforest), and alpine regions separates the subpopulations which may be a barrier to dispersal (Jones et al., 2004; Rose et al., 2017). Devils prefer open forest and woodlands without much ground level shrub, to facilitate hunting, but are also attracted to predictable point sources of scavengeable food such as garbage pits, "devil restaurants" for tourism, carcass dumps on farms, and roadkill (Jones, 2000; Rose et al., 2017). Additionally, areas with abundant prey, such as sheep pastures that are attractive to their primary native prey, macropods, often host the highest population densities of devils (Jones & Barmuta, 2000).

Importantly, the dark pelage and nocturnal activity of Tasmanian devils puts them at increased risk of WVCs as drivers may have more difficulty detecting these black-furred animals at night (Hobday, 2010). Devils are also noted to react unpredictably to headlights of oncoming vehicles (Hobday, 2010). Since devils are generalists and often forage along or are attracted to the roadway to scavenge on roadkill, they are increasingly vulnerable to becoming secondary roadkill themselves. Furthermore, as devils are marsupials, WVCs have the potential of causing greater loss if there are young carried in the pouch.

Roadkills are unfortunate outcomes of the intersection of human transportation requirements and ecological systems. However, as roads are a necessity for the foreseeable future, we must use data on the effects of existing roads to inform future conservation actions to mitigate any biodiversity loss stemming from roads. Though roads are widespread and easily accessible, they are usually an untapped source of ecological information. One of the most visible and accessible forms of this ecological data is roadkill. Although there is literature on localized studies of roadkill patterns for Tasmanian devils (Hobday & Minstrell, 2008; Jones, 2000; Kioko, Kiffner, Jenkins, & Collinson, 2015) there has been no large-scale study across the entire Tasmanian road network. To understand and predict devil WVCs to set conservation priorities, robust, spatially-explicit approaches that take ecological drivers into account are needed. Reliable modeling of predicted roadkill probability is invaluable to prioritization in mitigation and conservation action towards reducing Tasmanian devil WVCs. Previous roadkill research has explored predictive roadkill modeling by analyzing roadkill data with environmental and anthropogenic variables. Modeling approaches have included mainly regressions (Eberhardt, Mitchell, & Fahrig, 2013; Malo, Suárez, & Diez, 2004; Roger & Ramp, 2009; S. M. Santos, Lourenco, Mira, & Beja, 2013), including MaxEnt (K Chyn, Lin, Wilkinson, Tracy, & Fitzgerald, *in review;* Kantola, Tracy, Baum, Quinn, & Coulson, 2019; Yue, Bonebrake, & Gibson, 2019). As roads often have insidious effects on wildlife populations, and certain aspects of roads or areas surrounding roads can be more consequential than others, it is important to identify these factors.

Due to the threat of wildlife-vehicle collisions and subsequent road mortality to devil survival, our primary objective was to use the species distribution modeling tool (SDM) MaxEnt and devil roadkill records to predict the relative probability of roadkill across the Tasmanian road network, which we call roadkill risk, for future conservation action. In addition, we aim to describe the spatial patterns of devil roadkill in Tasmania, identify environmental and anthropogenic variables that contribute to roadkill risk, and develop a predictive roadkill risk tool to help conservation and transportation managers mitigate or prevent devil mortality on roads. Our study examined the influence of environmental variables on our power to predict the risk road mortality for the endangered Tasmanian devil. In previous studies, roads with high traffic speed and volume have been shown to have significantly higher wildlife roadkill (Hobday, 2010; Jaarsma, van Langevelde, & Botma, 2006; S.-C. Lin, 2016; van Langevelde & Jaarsma, 2005), and thus we expect road classes with these characteristics to have the highest devil road mortality risk (Hobday, 2010; Lester, 2015). We also expected that the presence of roadkill will be an important risk factor for devils, as devils are scavengers and may be attracted to this reliable source of food and increasing their risk of becoming secondary roadkill (Rose et al., 2017). Devil roadkills have also been observed on roads that divide forest-grassland ecotones (Save the Tasmanian Devil Program researcher, personal communication, July 2019), so we expected this environmental variable to have a relatively high effect on devil roadkill risk (Andersen et al., 2017). Lastly, we expect regions with higher human activity, such as urban areas and regions with more roads, will have more road mortality due to higher likelihood of interaction. Our modeling approach also allowed us to develop an intuitive interactive roadkill risk map, which we consider a useful conservation and management tool for conservation managers. We provide novel use of MaxEnt to predict roadkill mortality for devils across the

Tasmanian road network utilizing citizen science roadkill observations. The results will be used to inform transportation management and to make recommendations to reduce the ecological impacts of roads on Tasmanian devils.

4.3. Methods

4.3.1. Study Area

Tasmania is Australia's smallest state with an area of approximately 68401 km^2 and is separated from the mainland by the Bass Strait. At its narrowest Bass Strait is approximately 240 km wide and at its shallowest less than 70 m deep (Rawlinson, 1974). In contrast to mainland Australia, which is the driest inhabited continental land mass, Tasmania is temperate and maritime with mild winters and cool summers. It is the most mountainous state in Australia and the Central Highlands region extends over most of the central western parts of the state. The central eastern region is fairly flat and mainly used for agriculture. Tasmania also contains some of the last temperate rainforests in the Southern Hemisphere and is overall densely forested (Atlas, 2019). Tasmania also has a low human population density, approximately 7.6 people/km^2(Statistics, 2016), so the primary form of transport throughout the state is by road.

4.3.2. Data

4.3.2.1. Roadkill Data

Data for roadkill occurrences were obtained from Dr. Alistair Hobday (Hobday & Minstrell, 2008) and the Tasmanian Government - Department of Primary Industries, Parks, Water and Environment (DPIPWE)'s Save the Tasmanian Devil Program (STDP) (https://dpipwe.tas.gov.au/wildlife-management/save-the-tasmanian-devil-program). The former systematically collected wildlife roadkill data, including devils, from June 2001 to November 2004 within five general regions radiating out from Hobart, Tasmania. A total of 154 surveys were conducted and included major state and federal highways and secondary sealed roads. Each region was surveyed at least once per season, and seasonal surveys were assumed to be independent due to short persistence periods of carcasses on roads (Hobday & Minstrell, 2008). The roadkill data from the STDP, which comprises opportunistic wildlife roadkill data collection from volunteers and experts, was collected from February 2003 to December 2018. Data from STDP is filtered by reliability and accuracy. Reliability is a high likelihood that the animal was a devil and is given a binary assignment based on the status of the observer – observers who have had training, reports from the public which were accompanied by a quality photo, and Tasmanian devil biologists are given a "reliable" status, whereas all other observers are "not reliable." Locational accuracy (in metres) was estimated at the time of entry to the database, based on the location details provided in the report. Additionally, STDP also provided a separate database of wildlife roadkill obtained through reports to the Roadkill TAS app (https://dpipwe.tas.gov.au/wildlife-management/save-the-tasmanian-devil-program/about-the-program/roadkill-project/roadkill-tas-app) and were not checked as rigorously as the devil observations were.

The data from Dr. Hobday included a total of 47 devil observations, and we utilized all observations in our study as they were reliable and accurate. When acquired on January 10th, 2019, the STDP data contained 4192 observations of devil roadkill. After filtering observations to only include those from reliable observers and location accuracies of <50 m there were 166 observations remaining. In total, there were 213 devil roadkill observations with high accuracy and reliability used in our analyses. Additionally, when combined, both sources of roadkill data amassed 11454 Tasmanian wildlife roadkill observations with geospatial coordinates, excluding Tasmanian devils. All devil and wildlife roadkill points that were within 100 m of the road network were set to the closest center of a road. This allowed us to account for inaccuracies in GPS location from smart phones and reduced the data to 205 total devil observations.

4.3.2.2. Road Network

We cleaned the road network data obtained from the Land Information System Tasmania (LIST) to contain only segments categorized as "Road" transportation type (Table 1) – this transportation type includes defined paths primarily for cars and other general vehicles. The road network was categorized into road classes (Table 2) and we converted the individual road class shapefiles to 50 m x 50 m rasters.

4.3.2.3. Environmental Covariates

We analyzed 27 environmental covariates for our predictive roadkill risk maps (Table 3) that were generated from the following sources: the LIST provided sub-meter resolution land use (Australian Land Use and Management Classification (version 8) (ALUMv8)), a 25 m resolution digital elevation model (DEM), and vegetation (TASVEG 3.0) data. In both the ALUMv8 and TASVEG 3.0 datasets, we combined similar and redundant categories and chose variables that are ecologically relevant to Tasmanian devils. Slope was calculated from the 25 m DEM. As devils are a wide-ranging habitat generalist, covariate resolution can be coarse; many of the variables chosen were originally defined by the ALUMv8 and TASVEG 3.0 authors as coarser, more encompassing levels (see Supplemental Material xx).

We were also interested in the effect of the ecotone between forest and grasslands, as devils have been anecdotally noted to travel between these habitats (C. Lawrence, pers. obs.), so we created a forest-grassland ecotone variable from the TASVEG 3.0 and ALUMv8 data. To create this layer, we extracted two groups pasture and grasslands, and forest and woodlands, and ran a Euclidean distance tool to 100 m for each group. Areas where these groups overlapped were assigned as a "forest-grassland ecotone."

We also included Estimated Resident Population (ERP) data from the Australian Bureau of Statistics, which was provided in the Australian Statistical Geography Standard (ASGS) Statistical Areas Level 2 (SA2) resolution. Non-devil wildlife roadkill observations were included as a covariate as devils tend to scavenge on roadkill (Rose et al., 2017). We created a raster layer of the count of the non-devil wildlife roadkills within each 50 m x 50 m cell as a wildlife roadkill covariate. Additionally, road classes (Table 2) were included as covariates. We conducted pre-model fitting covariate selection by testing for correlations between our variables, and all values were <0.8 for the 27 variables, so all variables were kept in the model. Additionally, all non-categorical variables were standardized to aid in model fitting and result interpretation.

After selecting our environmental covariates, we converted the polygon shapefiles to 50 m x 50 m rasters for each covariate. We calculated percentage cover to capture the spatial effect of vegetation covariates up to 550 m outside of its delineated area. A 550 m x 550 m moving window was chosen because ecological studies on devils report large home ranges averaging 13.2 km^2 and neighborhood sizes of 100 km (Rose et al., 2017) and pass through many environments, so we account for a spatial effect of these environmental covariates up to 0.5 kms from the covariate areas themselves to account for possible push/pull factors of the covariates on devils. We used the "focal" function in the *raster* R package to create percent cover layers.

For covariates relating to bodies of water and bridges (Table 3), we calculated Euclidean distance. Water features are generally attractive to fauna and distance to water may have ecological spatial effects (Coffin, 2007; Farmer & Brooks, 2012; Hobday, 2010; Langen, Ogden, & Schwarting, 2009). We also calculated slope from the 25 m DEM and resampled the raster to 50 m resolution. Human population was rasterized to 50 m resolution from the SA2 level shapefiles. Lastly, the wildlife roadkills within a 50 m x 50 m raster cell were counted and assigned as values. We masked all of the covariate gradients to the rasterized Tasmanian road network. This is to constrain the roadkill model to areas where fauna-vehicle interactions are expected. Analyses were run with all variables projected in Asia South Albers Equal Area Conic projection.

Table 4.1 Data and data sources

Data	Data Source
Wildlife roadkill occurrences	Alistair Hobday; Save the Tasmanian Devil Program
Road network (transport segments)	Land Information System Tasmania (LIST) - Land Tasmania, DPIPWE
Digital Elevation Model (DEM) 25 m	Land Information System Tasmania (LIST) - Land Tasmania, DPIPWE
TASVEG 3.0 (vegetation)	Land Information System Tasmania (LIST) - Land Tasmania, DPIPWE
Australian Land Use and Management Classification version 8 (ALUMv8)	Land Information System Tasmania (LIST) - Land Tasmania, DPIPWE
Human population estimate	Australian Bureau of Statistics

Table 4.2 Categorical road classes

Road Code	Road Class
1	Access Road
2	Arterial Road
3	Collector Road
4	Local Road
5	National/State Highway
6	Sub Arterial Road
7	Vehicular Track

Table 4.3 Model covariates and covariate importance measurments

Environmental covariate	Covariate raster type	Percent contribution	Permutation importance
All wildlife roadkill	count	0.6	0.7
Forest-grassland ecotone	distance	1.8	0.7
Human population density	continuous	1.3	2.5
Animal farming	percent cover	0	0
Animal grazing	percent cover	1	2.5
Forestry	percent cover	0	0
Mining	percent cover	0	0
Waste	percent cover	0	0
Water	distance	0.4	0.7
Bridges	distance	5.8	5.6
Road class	categorical	53.5	51.3
Road density	continuous	1.4	8.6
Slope	continuous	7.3	7.7
Agricultural land	percent cover	2.7	3.9
Dry eucalypt forest	percent cover	1.1	1.4
Non-eucalypt forest	percent cover	1	0.4
Highland treeless vegetation	percent cover	0.7	0.8
Moorland, sedgeland, rushland, & peatland	percent cover	0.5	0.6
Native grassland	percent cover	1	2.1
Permanent easement	percent cover	0.2	0.6
Plantations for silviculture	percent cover	0.1	0
Rainforest & related scrub	percent cover	0.1	0
Regenerating cleared land	percent cover	0.2	0.2
Saltmarsh and wetland	percent cover	0.1	0.1
Scrub, heathland & coastal complexes	percent cover	7.7	3.7
Urban areas	percent cover	10.8	4.2
Wet eucalypt forest	percent cover	0.8	1.4

4.3.3. Analysis

Methods for this analysis are adapted from predictive roadkill risk modeling methodology developed in Chyn et al. *in review*, and methods are explained below. However, this study focuses on one species of conservation need and tailors the model covariates to its life history and ecology accordingly.

We related roadkill records to environmental covariates to predict roadkill distributions, or "roadkill risk," across a road network, using methodology adapted from Chyn et al. (2019). Methods for quantifying roadkill patterns generally fall within aggregation (or clustering) and predictive modeling (K. Gunson & Teixeira, 2015). As species distribution models can both identify the variables that best explain presence of roadkill and extrapolate predictions of relative roadkill rates into areas without observations, we believe it demonstrates advantages over hotspot and clustering roadkill analyses which can only highlight spatially clustered data. Previous studies have used various models for predicting roadkill risk (Gomes, Grilo, Silva, & Mira, 2008; K. E. Gunson, Mountrakis, & Quackenbush, 2011; Malo et al., 2004; Ramp, Caldwell, Edwards, Warton, & Croft, 2005), but few studies have employed MaxEnt for vertebrate road mortality (K Chyn et al., *in review;* Garrote, López, López, Ruiz, & Simón, 2018; Ha & Shilling, 2017; Kantola et al., 2019; Y.-P. Lin et al., 2019; Yue et al., 2019).

We chose to use MaxEnt (Phillips, 2005), one of the most widely used SDMs (Elith et al. 2011), for our predictions as it can be applied to presence-only datasets, like roadkill, and incorporates regularization to reduce overfitting, which facilitates the use of a large number of covariates (Merow, Smith, & Silander, 2013). We used the R package ‘*zoon’* (v0.6.3) (Golding et al., 2017) to create a reproducible workflow for our SDM analyses. MaxEnt uses maximum entropy estimation to fit a model to data (for details, see Merow et al., 2013). We employed all available MaxEnt feature types (linear, quadratic, hinge, threshold, and product) as more than 80 devil presence points were available (Merow et al., 2013). MaxEnt is a presence-background modeling method, so we generated 10,000 background points using a bias layer to account for sampling bias (Dudík, Phillips, & Schapire, 2006; Phillips et al., 2009). As the nature of roadkill confounds the state and observation processes we could not estimate sampling effort across the landscape directly, thus we used data on roadkill for all species across the road network to generate a bias layer (Jane Elith, personal communication, 7 May 2018) (Merow et al., 2013). Our bias layer was created using a two-dimensional kernel density estimate based on the coordinates of roadkill presence points of all wildlife species, including devils, to account for sampling bias. This was then masked to the road network. This means that our background samples were generated with the same biases inherent in the wildlife presence data. By accounting for sampling bias we assure the same environmental biases in both presence and background data (Dudík et al., 2006; Phillips et al., 2009). We also selected additional options for jackknife and variable percent contribution analyses as measures of variable importance.

4.3.4. Model Evaluation

We ran 10-fold cross-validation (k = 10) on the model and used the Area Under the Receiver Operating Characteristic Curve (AUC) evaluation metric to assess model performance. Cross-validation is especially helpful for SDMs when there is no independent dataset available to validate model predictions. In our analysis, the data was split into 10 dataset folds, and we fit a model to every possible combination of 9 folds, known as the training dataset, and then evaluated the model's predictions on the remaining hold-out fold, known as the testing data. The continuous projections of the 10 MaxEnt training set models were combined by averaging to create a training set ensemble (TSE) model. The AUC was used as a metric to evaluate performance for all models when data was cross-validated as it is a threshold-independent and scale-invariant metric that can be used for presence-only models. We calculated the test AUC, training AUC, the overfitting statistics of AUC difference (AUC_{diff} = training AUC – test AUC) and the minimum and 10^{th} percentile training presence threshold omission rates (Radosavljevic, Anderson, & Araújo, 2014; Warren & Seifert, 2011) to test for overfitting. We chose to report variable importance as a measure of permutation importance rather than percent contribution, as permutation importance has been shown to be a more accurate and reliable predictor for variable selection accuracy (Halvorsen, 2013; Searcy & Shaffer, 2016).

For all above analyses, we used the following programs and R packages: R 3.5.1 (Team, 2017), QGIS 3.6 (QGIS Development Team , 2019), ArcGIS 10.61, MaxEnt 3.4.1 (Steven J. Phillips, Miroslav Dudík, & Schapire, 2017), '*zoon*' (Golding et al., 2017), *dismo* (Robert J. Hijmans, Steven Phillips, John Leathwick, & Elith, 2017), and '*caret*' (Max Kuhn. Contributions from Jed Wing, Engelhardt, & Lescarbeau, 2018).

4.4. Results

The 213 Tasmanian devil roadkill records were spread sparsely across Tasmania (Fig. 4.1), likely due to a large area and an equally sparse road network. We produced a predictive roadkill risk map for the endangered Tasmanian devil (an interactive version of this figure, which allows users to zoom in on specific regions is available in Appendix B). We also identified several environmental variables that best explained the presence of roadkill for devils.

The predictive map for devils showed road sections with higher risk of road mortality were not concentrated in any particular geographic region (Fig. 4.2). Instead, the high-risk areas were spread sparsely throughout Tasmania, with few specific areas indicated as high-risk (Fig. 4.3). Highest roadkill risk areas were predominately ununiformly distributed across Tasmania's national and state highways. The following covariates had the highest permutation importance: road class, road density, slope, bridges, and urban areas (Table 3). We are choosing to place emphasis on permutation importance over percent contribution, as permutation importance has been shown to be a more accurate and reliable predictor for variable selection accuracy (Halvorsen, 2013; Searcy & Shaffer, 2016). The model had the following performance metrics: test AUC = 0.918, training AUC = 0.944, and the AUC_{diff} = 0.026. The minimum and 10th percentile training presence threshold omission rates were 0.000 and 0.099, respectively. As they were not higher than the theoretical expectation for the respective thresholds, 0% and 10%, they do not indicate overfitting for the model.

The road class variable had the highest permutation importance. As road class is a categorical variable, the classes of roads that most strongly influenced roadkill probability devils were national/state highways, arterial roads, and sub-arterial roads, respectively (Table 2). Additionally, the model had a very high AUC and low overfitting statistic, which suggests the high AUC metric was not due to overfitting.

Clear associations between environmental variables and road mortality of devils were revealed in the MaxEnt model. Overall, the environmental variables with the highest permutation importance to road mortality points across taxa were related to characteristics of roads and urbanization.

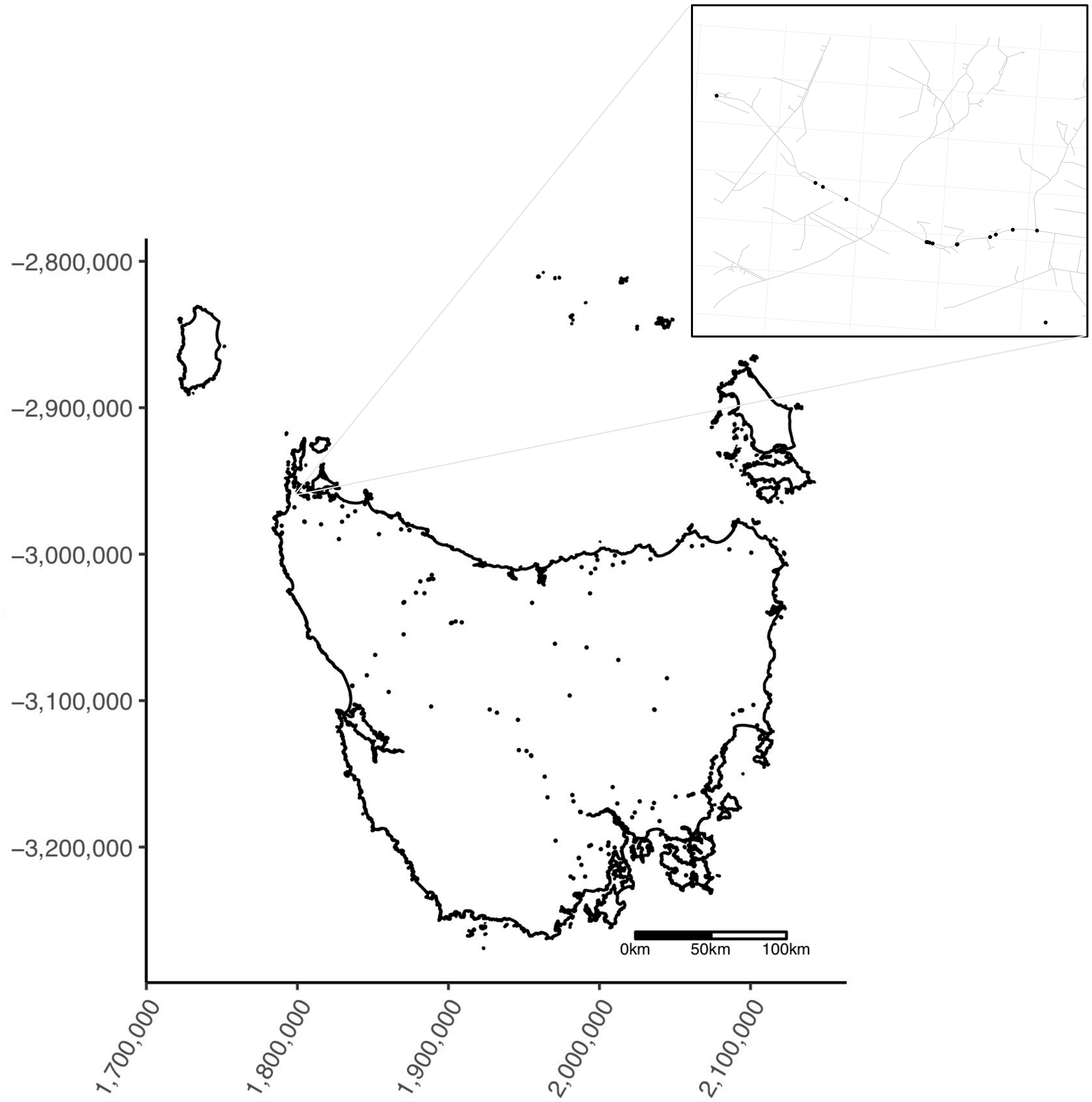

Figure 4.1 Map of Tasmanian devil (Sarcophilus harrisii) 213 roadkill occurrences and inset with the extent of x (1800000, 1808000) and y (-2962000, -2956000) in the Asia South Albers Equal Area Conic projection. Black dots represent devil roadkill occurrences, dark gray lines in the inset represent the road network, light gray lines represent the map grid.

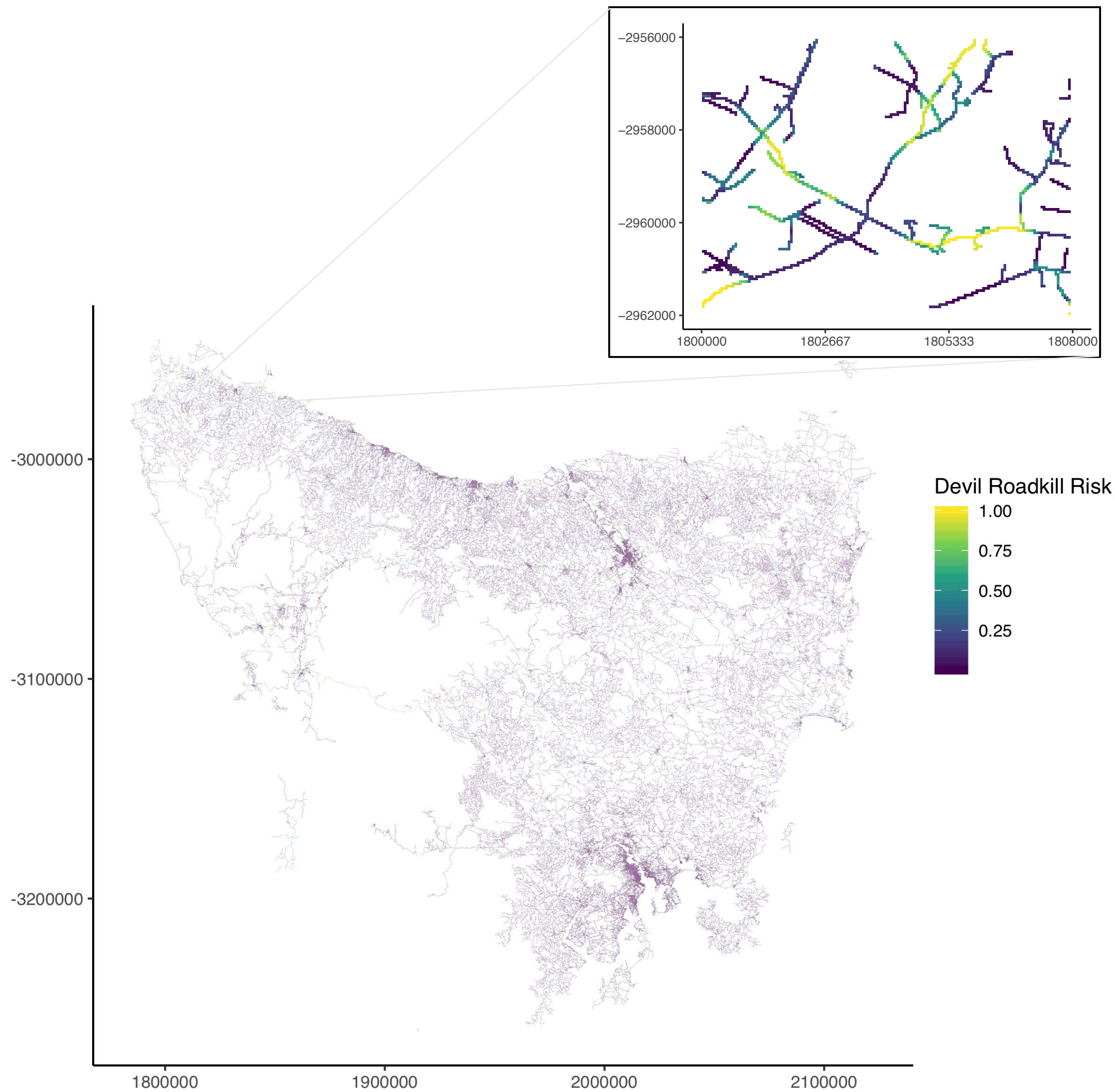

Figure 4.2 Tasmanian devil (Sarcophilus harrisii) predictive roadkill risk map and inset with the extent of x (1800000, 1808000) and y (-2962000, -2956000) in the Asia South Albers Equal Area Conic projection. Yellow values denote predicted high roadkill risk and purple values denote predicted low roadkill risk.

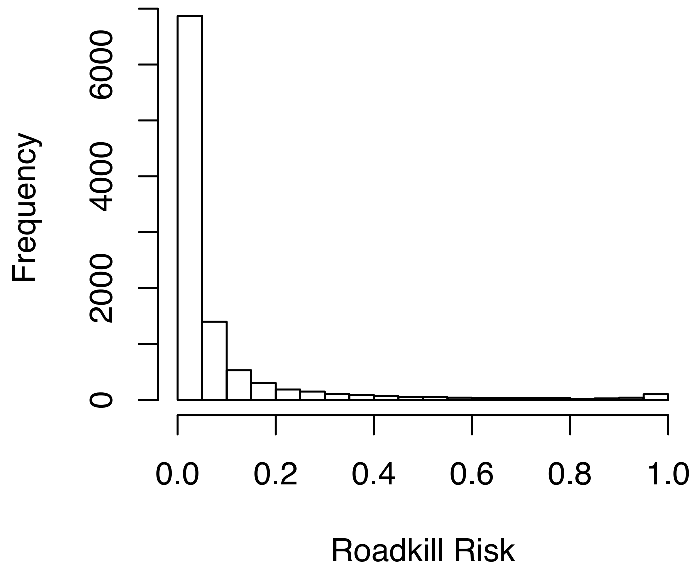

Figure 4.3 Histogram of model roadkill probability predictions.

4.5. Discussion

As Tasmanian devil genetic diversity is considered low (Jones et al., 2004), and devils have seen a total population decline of 85%, each remaining individual is important to the conservation of the species. Cutting the loss of individuals due to preventable deaths, such as roadkill, is a paramount conservation priority. We modeled the predictive roadkill risk for the endangered Tasmanian devil across the Tasmanian road network. This work highlights the utility and importance of collecting devil roadkill data, as it can greatly contribute to informing immediately applicable conservation action. A tangible outcome of this research is a predictive mapping tool for conservation practitioners and transportation managers for immediate use in actionable mitigation of the impacts of WVCs on Tasmanian devils.

Our study resulted in novel findings on areas of predicted high and low risk of WVCs for devils and identified which environmental variables, including variables about the roads themselves, contributed most to high roadkill predictions. As hypothesized, we also found that road classes were the most important variable in predicting Tasmanian devil roadkill and that the national/state highway class had higher risk than other classes. Road class serves as a proxy for traffic speed and volume data and broadly defines those traffic characteristics. Of the seven road classes included in our analyses (Table 2), the national/state highway class had the highest capacity for vehicular traffic and speed. The second and third most important road classes were arterial and sub-arterial road classes, which are also the second and third largest road classes, respectively. This pattern suggests that roads with high traffic volume and speed exhibit greater risk of devil roadkill, which is corroborated by previous studies (Hobday, 2010).

Surprisingly, the presence of other wildlife roadkill and proximity to a forest-grassland ecotone both did not greatly influence the presence of devil roadkill risk (Table 3). These variables, though important to devil ecology (Andersen et al., 2017; Rose et al., 2017), did not have a large effect on the model relative to other factors, such as road class. This, however, does not suggest that the variables are not important to devil road mortality, as devil prey species use these ecotones for cover while foraging and devils use them to ambush live prey (Andersen et al., 2017). Prey fleeing from open grassland to forest cover on roads in this ecotone are also susceptible to WVCs, which in turn provides an attractive food source for devils. However, though ecotones are ecologically attractive to devils, they may not change devil behavior enough to effect roadkill risk and it holds relatively less importance than other variables. Additionally, the ecotone variable included may be too coarse to pick up small but ecologically relevant ecotones – for instance, a thick shelter-belt along a roadside in an otherwise pastured region could function like an ecotone with respect to animal behavior (forage on one side of the road, covered shelter on the other), but would not be represented in the coarser resolution ecotone variable.

Due to the low overfitting statistic and minimum and 10th percentile training presence omission rates within the theoretical expectation for the thresholds, there was no indication of overfitting for the devil roadkill risk model. Additionally, the histogram of the predicted roadkill risk probabilities (Fig. 3) contains the range of values from 0 to 1, also indicative that the model was not overfit. The histogram also suggests that most Tasmanian roads are not likely to have high Tasmanian devil roadkill risk relative to the rest of the Tasmanian road network, as a large proportion of predictions were zero. This is a potentially encouraging finding and means that conservation efforts can be focused on the small proportion of areas that we found to have high roadkill risk.

Though important, predictive modeling based on SDMs is not without its caveats (Araujo & Guisan, 2006; Barry & Elith, 2006; Jarnevich et al., 2018) . Due to the nature of presence only and opportunistic roadkill data, variability in detection of roadkill may occur which can introduce spatial, taxonomic, or temporal bias. Our dataset was also filtered with stringent standards, so the data used for modeling was a subset of a large database, which may also introduce sampling bias. Opportunistic datasets are incomplete and do not comprehensively cover geographic and/or environmental space, so predicting roadkill probability in areas without observations is especially valuable. We accounted for these potential issues by using biased background points in the models to capture the nature of sampling bias. Datasets on effort to collect roadkill data would allow further enhancement of predictive roadkill models, however, like most other roadkill data, our dataset did not quantify sampling effort. Additionally, roadkill often goes unnoticed or unreported for a variety of reasons that are dependent on observer, the environment, and other ecological sources (Kristina Chyn, Lin, Chen, Chen, & Fitzgerald, 2019; S M Santos, Carvalho, & Mira, 2011; Skórka, 2016). Other studies showed correlations between traffic volume and traffic speed with devil roadkill (Hobday & Minstrell, 2008); however, we were unable to acquire this data for the entire Tasmanian road network. We believe covariates such as road class and human population estimates could serve as proxies for these covariates in future studies.

Population density of devils may have biased roadkill in areas with healthier populations of devils. However, the claim of faunal density affecting roadkill levels has not been tested on a landscape scale. In one study where live faunal density was surveyed to test for a relationship with roadkill density, there were no significant trends between density of live Tasmanian fauna and roadkill at local scales, though faunal density varies widely across Tasmania (Hobday & Minstrell, 2008). Lastly, as devils are nocturnal, we expected most WVC incidents occurred at night and did not include activity period as a variable. However, Hobday (2010) did show that in some cases darkness did increase risk of devils being hit due to lower driver reaction time.

Additionally, large, fast, industrial vehicles with low visibility (logging trucks, milk tankers) often travel between dusk and dawn.

Our recommendations for mitigation and prevention of Tasmanian devil WVCs echo many recommendations from the broader roadkill mitigation literature (Smith, Van Der Ree, & Rosell, 2015; van der Ree, Gagnon, & Smith, 2015; van der Ree, Smith, & Grilo, 2015). As the variable that contributed the most to devil roadkill was road class, most mitigation measures should focus on roads themselves. Because the national/state highways with high traffic speed and volume had the most roadkill, we suggest that Tasmania reduce driver speeds in the areas where our model and maps show devil roadkill is predicted to be highest, especially at night. It has been shown that areas with vehicle speed limits that exceeded 80 km/h contained more than 50% of the state's roadkill (Hobday, 2010), and many highways in Tasmania have speeds up to 110 km/h. Additionally, an essential component of mitigation for all WVC mitigation is fencing paired with crossing structures (e.g. culverts) (van der Ree, Gagnon, et al., 2015). High-risk areas highlighted by the model can be amended with fencing along both sides of the road leading to a culvert or overpass for devils to be funneled into. Specifically, small underpasses (300-450 mm diameters) are recommended for Tasmanian mammals with smaller body sizes that use burrows, such as devils (Magnus, Kriwoken, Mooney, & Jones, 2004). However, structures to allow for escape from between fencing need to be provided as devils often travel along roads. Currently, several local councils have also installed "virtual fencing," a system of devices designed to alert devils and other wildlife to oncoming vehicles with sensory alarms (Lawrence & Wiersma, 2019). These have been successful in reducing roadkill in regions of Tasmania (Fox, Potts, Pemberton, & Crosswell, 2019), and further testing in high roadkill risk areas should be considered. We suggest at minimum that the above WVC mitigation strategies can be implemented on high risk areas targeted by our model in conjunction with an adaptive management plan. Additionally, the lack of systematically collected roadkill data across the entire Tasmanian road network makes it difficult to ground-truth the model prior to mitigation implementation. Future studies on ground-truthing predicted high devil roadkill risk areas, continued monitoring, and adaptive management are necessary in Tasmanian devil roadkill mitigation.

There is a necessity for large landscape-scale roadkill research in road ecology (van der Ree, Jaeger, van der Grift, & Clevenger, 2011). This first island-wide predictive roadkill risk model for Tasmanian devils will help in the tremendous conservation efforts for this enigmatic and endemic species. This modeling methodology is not limited to location, species, or even ecological hierarchy (K Chyn et al., *in review*), and can be tailored to a range of ecological questions. The utility of this model for other species of conservation concern is only restricted by the quality of roadkill data, which is relatively accessible and easy to collect.

4.6. References

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5. CONCLUSIONS

5.1. Conclusion

The central theme of my doctoral dissertation was the intersection of ecological and anthropologic structures through the lens of the effects of roads on wildlife in insular systems. I followed the precedent of descriptive studies by quantifying the magnitude of roadkill in Chapter 2 for Taiwan, as well as developed a novel use of an SDM utilizing citizen science data to predict relative road mortality risk in Chapters 3 and 4, for wildlife in Taiwan and Tasmania, respectively. In describing patterns of roadkill in Taiwan, I elucidated important insights, as there are groups and species that are highly and disproportionately affected by roads. For example, my work showed snakes are particularly vulnerable to roadkill, and my results hopefully inspire others to begin taking the threat of roadkill to snakes very seriously. In the predictive roadkill risk studies, the models ranged in ecological scale from species to functional guild. I've demonstrated that the predictive roadkill risk models I've developed can be tailored for ecological questions and scaled accordingly. I have also demonstrated the global scalability of this predictive roadkill risk methodology, which is only dependent on accumulation of quality roadkill observations and widely available environmental data. As such, this research has highlighted the importance and utility of roadkill data collection for conservation, especially through large citizen science programs.

Accumulation of well-organized roadkill data are especially important for threatened guilds, such as terrestrial turtles (Chen, Lin, Lin, & Yang, 2017; Lin, Wu, Lin, Mao, & Chen, 2010; Zhao, 1998; Zhihua Zhou & Jiang, 2008) and semi-aquatic and aquatic snakes in Taiwan (Chen et al., 2017; Mao, 2004). Moreover, roads and roadkill are a specific threat to the survival of certain species of great conservation concern, such as the endangered Maki's Keelback snake (*Hebius miyajimae*) (Z. Zhou, Lau, Jiang, & Lin, 2016) and Tasmanian devil (*Sarcophilus harrisii*) (Grueber et al., 2017). Roadkill data collected through volunteer citizen scientists has multiple benefits for researchers and the public: larger sample size, ecological education for citizens, national data-sets across multiple landscapes, and national governmental involvement with local expertise.

I studied the patterns of roadkill in Taiwan and Tasmania, Australia for several reasons. Firstly, they are both islands separated by narrow straits from a larger mainland, and they both host many threatened endemic wildlife species. In Taiwan, I elucidated the disproportionate effect of roads on threatened endemic species and groups (e.g. snakes) (Kristina Chyn, Lin, Chen, Chen, & Fitzgerald, 2019; K Chyn, Lin, Wilkinson, Tracy, & Fitzgerald, *in review*). I also focused my research on the Tasmanian Devil, an endemic species that also experiences large threat from roads, due to depleted populations (Lawrence & Wiersma, 2019).

Taiwan and Tasmania also differ in many important ways that could affect roadkill and predictive roadkill modeling; Taiwan has high road density (1.2 km of roads/km^2) and population density (approx. 667 people/km^2), and Tasmania has relatively low road density (0.106 km of roads/km^2) and population density (7.24 people/km^2) (CIA, 2017). These differences created apparent differences in patterns of predicted roadkill risk from Chapters 3 and 4; high roadkill risk areas for devils were sparsely distributed across the island's low density road network (Fig. 4.2, Appendix B1) and mainly occurred along stretches of highways, whereas high roadkill risk areas for guilds in Taiwan were spread widely across multiple road types (Figs. 3.2, 3.3, 3.4, Appendix A2), which may make it more difficult to identify areas for mitigation. Additionally, relative to Taiwan, Tasmania did not have as robust or established of a roadkill monitoring program, which adds challenges to the roadkill risk modeling process. The devil occurrences were not verified, so heavy filtering was required to obtain accurate (<50 m) and reliable data. Compared to the roadkill models for guilds and species of conservation concern in Taiwan, there may be sampling bias introduced from heavy filtering of devil data. As designed, these differences allowed me to test the applicability of my predictive models in contrasting systems. Understanding the powers and pitfalls of modeling in, in many ways, juxtaposing systems, tested the model for global adaptability. As we were successful in developing predictive roadkill risk models with high performance in both island systems and across ecological scales, these models have wide global applicability.

One of the most impactful findings from Chapter 2 was of the impact of wildlife-vehicle collisions on snakes in Taiwan. Snakes are highly and disproportionately killed on roads comprising 35% of the total confirmed roadkill observations in Taiwan and 50% of the protected species roadkill. Relatedly, warmer seasons had higher frequency of roadkills, especially for ectothermic taxa. Additionally, a small number of species accounted for most of the roadkill, where the top 23 most killed species comprised 50% of all confirmed roadkill occurrences. These groups that are highly and disproportionately affected by roads are in need of conservation action. This first synthesis of all data from the Taiwan Roadkill Observation Network (TaiRON) provided an understanding of the magnitude of roadkill in Taiwan to inform transportation and conservation managers in Taiwan and also following work in my dissertation.

In Chapters 3 and 4, I demonstrated this applicability and scalability of the predictive roadkill risk modeling methodology both globally, across the highly contrasted systems in Taiwan and Tasmania, and ecologically, across species and guild-level analyses. An interesting challenge in applying the methodology for the species-specific Tasmanian devil model from Chapter 4 was that there were fewer roadkill observations and they were spread across a comparatively sparse road network than Taiwan's guild-level models in Chapter 3. However, the high model performance in predicting devil as well as guild-level roadkill risks suggests global applicability of the methodology, even in areas with sparse roadkill data. A few caveats arose in modeling roadkill risk. First, though the methodology is scalable to ecological questions of interest, individual models must be produced for each species or guild of interest. This was demonstrated by the vastly different predicted relative roadkill risks across herpetofaunal guilds in Chapter 2. As these guilds were grouped by similar ecological function, threat, and conservation need, different environmental covariates, and thus, regions, had differing ecological influences on each guild's roadkill risk. Though this may be obvious for species-level models, groups for these models must be chosen thoughtfully, especially if they are to translate to successful and meaningful roadkill mitigation. This is especially important because this methodology implies that conservation and transportation planners and managers can model roadkill risk for mitigation wherever they have roadkill data for whichever species and groups they see fit. They can also model future road projections to find the least-cost scenario in terms of wildlife roadkill for the inevitable future road planning. Notably, interactive roadkill risk maps where users can explore the maps were developed for all guilds and species modeled (Appendix A2, B1), and they are an immediately valuable conservation tool for researchers and managers. These interactive maps can be downloaded for offline use and can be accessed from any computer or smart-device (phones and tablets) to study the details of roadkill risk models, also making them practical and functional in the field.

For reasons above, my findings revealed the importance of collecting roadkill data. As it is relatively low cost and low effort to collect data, especially when projects engage citizen science volunteers, roadkill can be an important and accessible source of ecological information. I modeled roadkill risk with three databases – one with wide participation from citizen scientists across Taiwan and verified data, another with structured data collection on a regional scale in Tasmania, and the last with unstructured and unverified data and lower participation across Tasmania. The data from TaiRON was collected in a structured format that allows for high accuracy of information, and data is verified by project managers (Kristina Chyn et al., 2019), so most of the opportunistic observations were reliably usable in the roadkill risk models. Similarly, structured data from Alistair Hobday (Hobday, 2010) were collected systematically by Tasmanian ecologists, so they were reliably usable, but data were only regionally collected. Data from the Save the Tasmanian Devil Program (STDP) were opportunistically collected by citizen scientists, but the data was unstructured and not always reliable or accurate, as observations were not verified by experts. Due to differences in data collection and databasing, a challenge arose when modeling Tasmanian devil roadkill risk; after filtering for reliability (expert or trained volunteer observations) and locational accuracy (within 50 m of accuracy), there were only 213 devil observations across Tasmania. Species distribution models may be problematic when implemented with species with fewer occurrences, however, these species are often those most in need of predictive modeling for conservation action (Gaubert, Papeş, & Peterson, 2006; Shcheglovitova & Anderson, 2013), such is the case with devils.

Though, ultimately, my methodology produced predictive roadkill risk models with good model performance, they likely would be enhanced with more verified devil roadkill occurrences. Thus, I suggest modeling roadkill observation programs after successful systems, such as TaiRON and others (Shilling, Perkins, & Collinson, 2015), and referring to the wealth of literature for citizen scientist data management (Devictor, Whittaker, & Beltrame, 2010; Dickinson et al., 2012; Dickinson, Zuckerberg, & Bonter, 2010; Kosmala, Wiggins, Swanson, & Simmons, 2016), volunteer participant engagement (Brossard, Lewenstein, & Bonney, 2005; Miller-Rushing, Primack, & Bonney, 2012; Toomey & Domroese, 2013), and specific roadkill methodology and projects (Cosentino et al., 2014; Langen et al., 2007; Langen, Ogden, & Schwarting, 2009; Marsh et al., 2017). These citizen science roadkill observation programs benefit both the public and conservation research greatly, and they are a worthwhile investment for informing roadkill mitigation.

Future studies can build on this research in several important ways. First, systematic citizen science roadkill observations, with both presence and absence observations, should be explored worldwide, and studies of patterns of wildlife roadkill similar to Chapter 2 should be pursued. Secondly, ground-truthing the high predicted roadkill risk areas highlighted in Chapters 3 and 4 should be conducted as further model validation. Third, once enough systematic presence/absence roadkill data is collected, roadkill risk models should be created using both roadkill presence and absence data, which is potentially more accurate than presence only modeling as sampling bias is accounted for (Phillips et al., 2009). Additionally, with presence/absence roadkill data, a new host of species distribution models (SDMs) beyond MaxEnt are available to explore (Elith & Leathwick, 2009), and roadkill risk should be modeled using a range of SDMs to elucidate those that are best employed in roadkill risk prediction.

Even during the early advent of cars, ecologists like Joseph Grinnell forecasted the impeding impact of roads on wildlife. Regarding road mortality in his Death Valley, California field notes, Grinnell stated that "this [roadkill] is a relatively new source of fatality; and if one were to estimate the entire mileage of such roads in the state, the mortality must mount into the hundreds and perhaps thousands every 24 hours" (Grinnell, 1920). [Personal aside: I was a passenger in an SUV that hit and killed a rabbit in Death Valley, California during the summer of 2010. We were traveling at the legal speed limit between 60-70 mph.] Since the 1920s, cars and roads have only increased in volume, density, and speed, and the impacts of roads on wildlife have correspondingly grown in magnitude. It is important that our research and efforts to mitigate these impacts of vehicles and roads on wildlife grow at a similar scale. In this dissertation, I incorporated both large crowdsourced datasets and predictive modeling methods to develop ecologically attuned tools for applied conservation in road ecology on a landscape-scale. I quantified patterns of roadkill and elucidated wildlife groups that are most heavily impacted in Taiwan and develop a novel methodology to model predicted relative roadkill risk across a road network for species and guilds of conservation concern in Taiwan and Australia. I tested whether this modeling method was scalable, both ecologically (from species to guilds) and globally (in two contrasting systems). My research identified recommended areas for mitigation in a spatially explicit and predictive context. The outcomes of my research have produced interactive predictive roadkill tools for collaborators and managers and will continue to be fruitful for wildlife conservation globally.

5.2. References

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APPENDIX A

Appendix A1 Example of *zoon* workflow for turtle guild:

```
Turtles <- workflow(occurrence = LocalOccurrenceDataFrame(turtles, columns = c(long = 'longitude', lat
= 'latitude', value = 'value'),
                    occurrenceType = "presence"),
                    covariate = LocalRaster(rasstack),
                    process = Chain(StandardiseCov(exclude = "roadtype_ras_50_msk"),
                    Background(10000, bias = occur.bias), Crossvalidate(k = 10)),
                    model = MaxEnt(args = c("-J", "-P", "noautofeature"), factors =
                    "roadtype_ras_50_msk", path = 'figures/output_ME/turtles/'),
                    output = PrintMap)
```

Appendix A2 Predictive roadkill model interactive maps as .html files. All .html files can be found in the following GitHub repository (https://github.com/kmchyn/2019_TW_roadkill-risk). Each guild and species also have the .html file hosted as a website.

A2.1 The Common Venomous Snakes (CVS) interactive predictive roadkill model interactive map .html file can be found in the Github repository (https://github.com/kmchyn/2019_TW_roadkill-risk/blob/master/com_ven_snk.html) and is hosted as a website (https://rawcdn.githack.com/kmchyn/TW_risk/94f2b73b85350f54704f6a42e2eaa3d49e4e49a6/com_ven_snk.html).

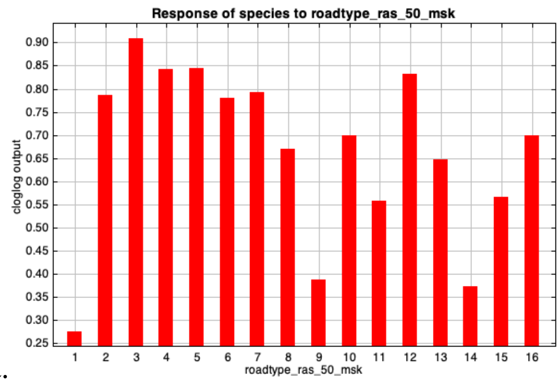
A2.2 The Semi-aquatic and Aquatic Snakes (SAS) interactive predictive roadkill model interactive map .html file can be found in the Github repository (https://github.com/kmchyn/2019_TW_roadkill-risk/blob/master/semi_aqu_aqu_snk.html) and is hosted as a website (https://rawcdn.githack.com/kmchyn/TW_risk/94f2b73b85350f54704f6a42e2eaa3d49e4e49a6/semi_aqu_aqu_snk.html).

A2.3 The turtle interactive predictive roadkill model interactive map .html file can be found in the Github repository (https://github.com/kmchyn/2019_TW_roadkill-risk/blob/master/turtles.html) and is hosted as a website (https://rawcdn.githack.com/kmchyn/TW_risk/94f2b73b85350f54704f6a42e2eaa3d49e4e49a6/turtles.html).

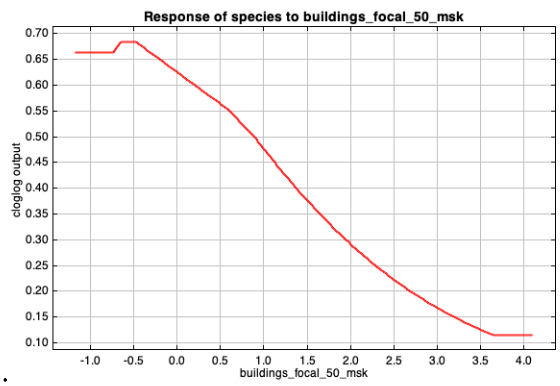
A2.4 The Maki's keelback snake (*Hebius miyajimae*) (HM) with k=10 cross-validation interactive predictive roadkill model interactive map .html file can be found in the Github repository (https://github.com/kmchyn/2019_TW_roadkill-risk/blob/master/A_miyajimae.html) and is hosted as a website (https://rawcdn.githack.com/kmchyn/TW_risk/94f2b73b85350f54704f6a42e2eaa3d49e4e49a6/A_miyajimae.html).

A2.5 The Maki's keelback snake (*Hebius miyajimae*) (HM) with k=n=50 cross-validation interactive predictive roadkill model interactive map .html file can be found in the Github repository (https://github.com/kmchyn/2019_TW_roadkill-risk/blob/master/A_miyajimae-50k.html) and is hosted as a website (https://rawcdn.githack.com/kmchyn/TW_risk/94f2b73b85350f54704f6a42e2eaa3d49e4e49a6/A_miyajimae-50k.html).

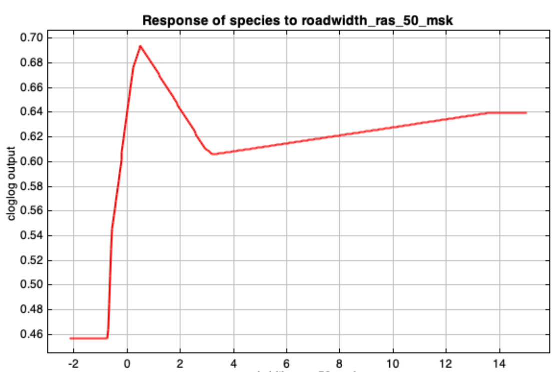
Appendix A3 Top five contributing variable response curves for Common Venomous Snakes, Semi-aquatic and Aquatic Snakes, Turtles, and both *Hebius miyajimae* models (k=10 and k=50), respectively.



a.

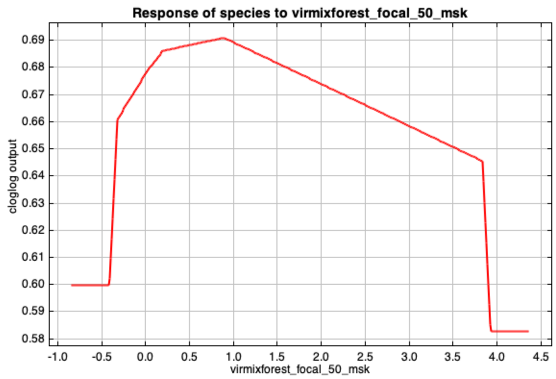


b.

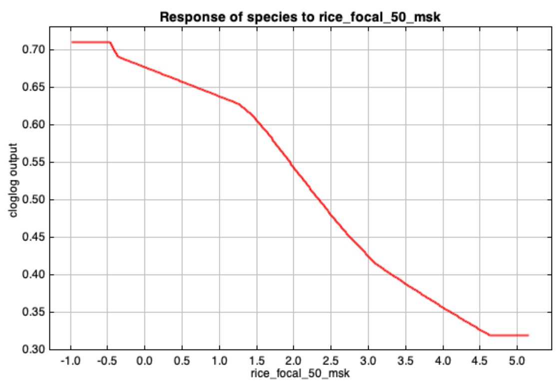


c.

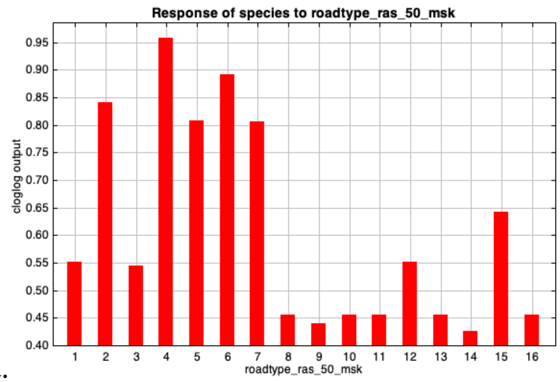
d.



e.

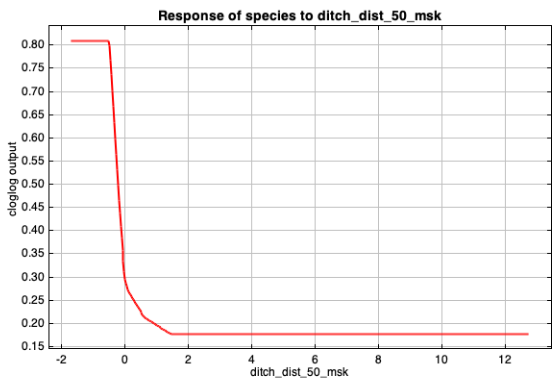


A3.1 a-e The top five contributing environmental variable response curves by permutation importance for the CVS roadkill risk model: a) road type, b) buildings, c) road width, d) virgin mixed forest, e) rice.



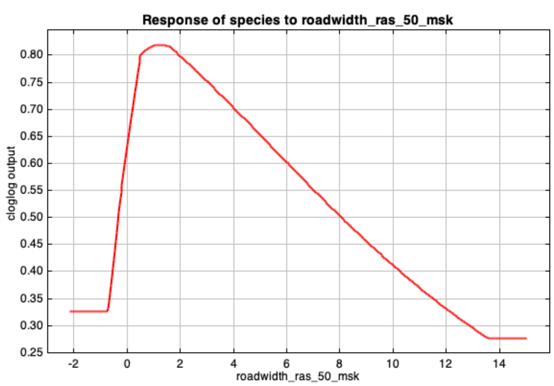
Response of species to roadtype_ras_50_msk
cloglog output
roadtype_ras_50_msk

a.



Response of species to ditch_dist_50_msk
cloglog output
ditch_dist_50_msk

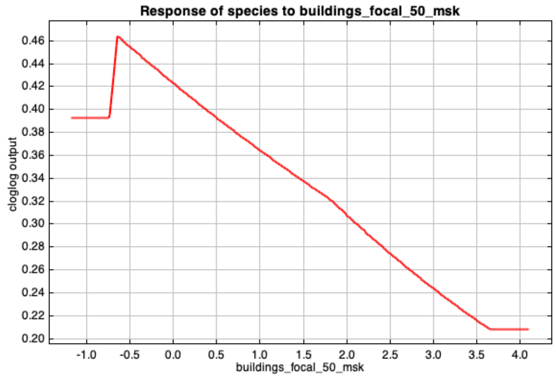
b.



Response of species to roadwidth_ras_50_msk
cloglog output
roadwidth_ras_50_msk

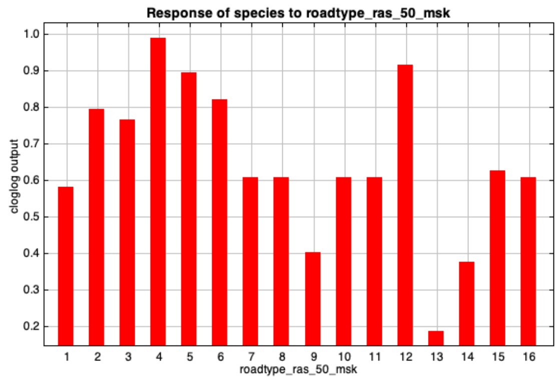
c.

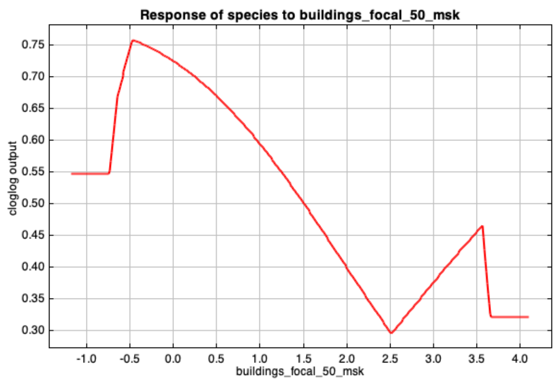
d.

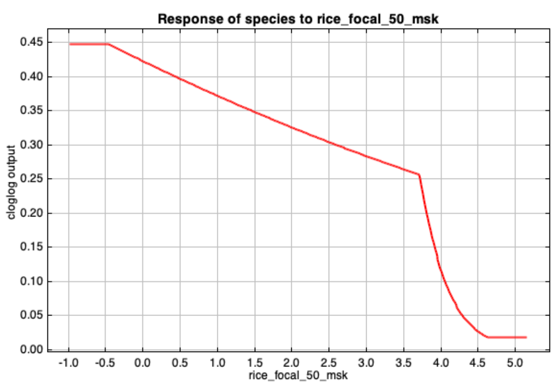


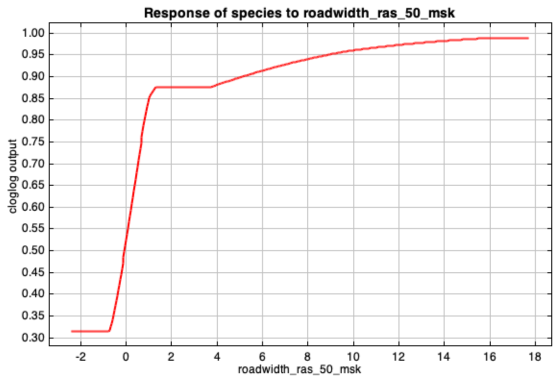
e.

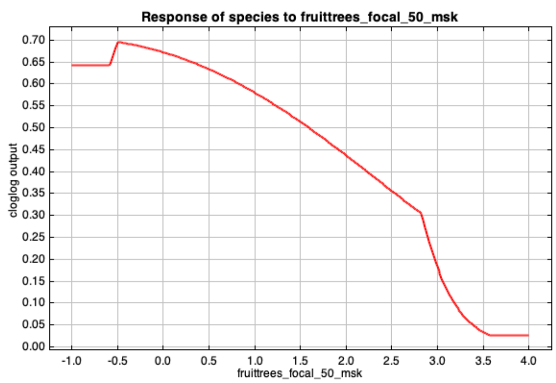
A3.2 a-e The top five contributing environmental variable response curves by permutation importance for the SAS roadkill risk model: a) road type, b) ditch, c) road width, d) buildings, e) beach wetland.


Response of species to roadtype_ras_50_msk
cloglog output
roadtype_ras_50_msk
a.

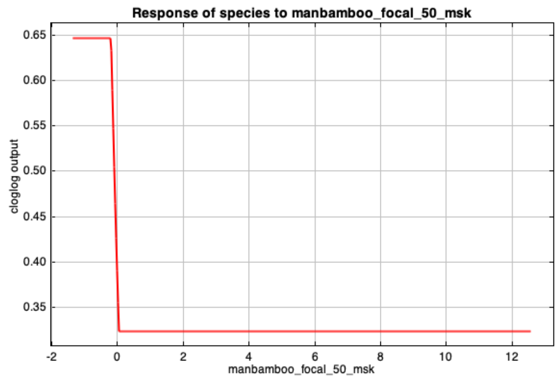

Response of species to buildings_focal_50_msk
cloglog output
buildings_focal_50_msk
b.


Response of species to rice_focal_50_msk
cloglog output
rice_focal_50_msk
c.

d. 

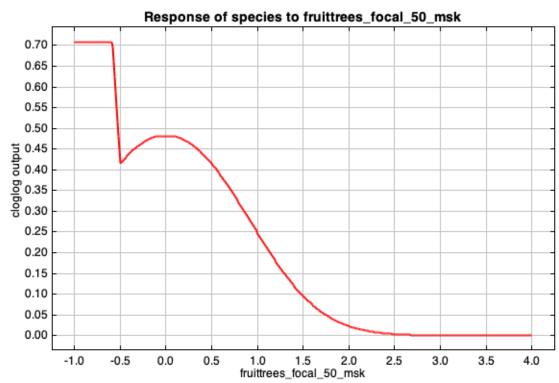
e. 

A3.3 a-e The top five contributing environmental variable response curves by permutation importance for the Turtle roadkill risk model: a) road type, b) buildings, c) rice, d) road width, e) fruit trees.



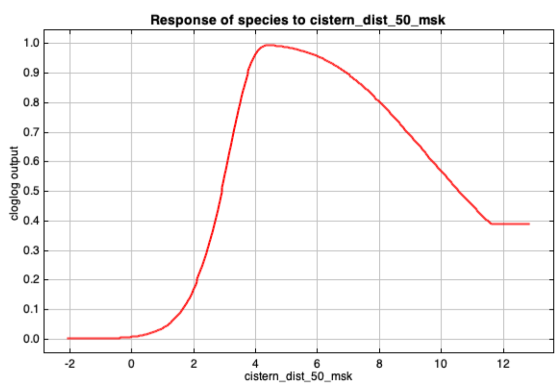
Response of species to manbamboo_focal_50_msk
cloglog output
manbamboo_focal_50_msk

a.



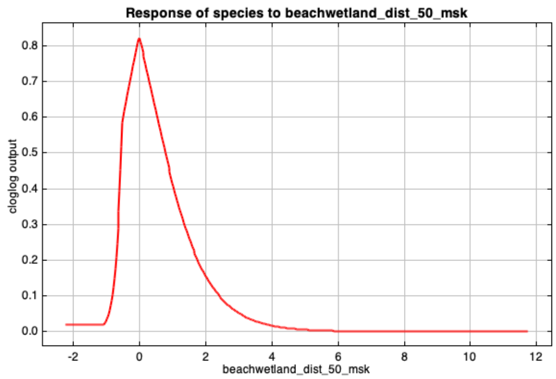
Response of species to fruittrees_focal_50_msk
cloglog output
fruittrees_focal_50_msk

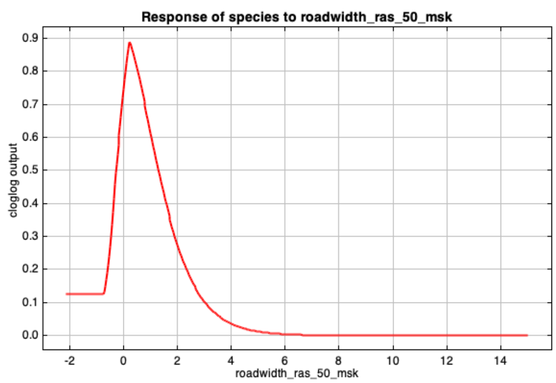
b.



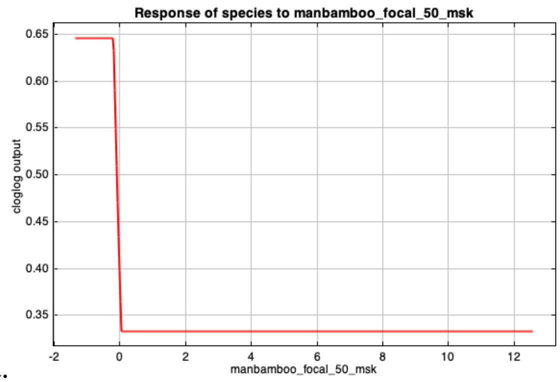
Response of species to cistern_dist_50_msk
cloglog output
cistern_dist_50_msk

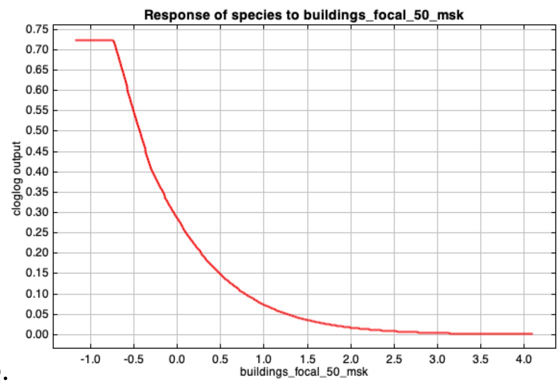
c.

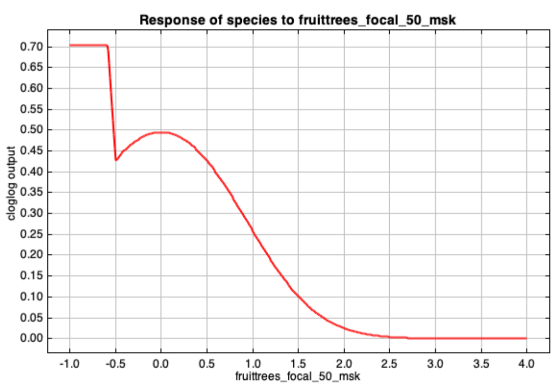
d. 

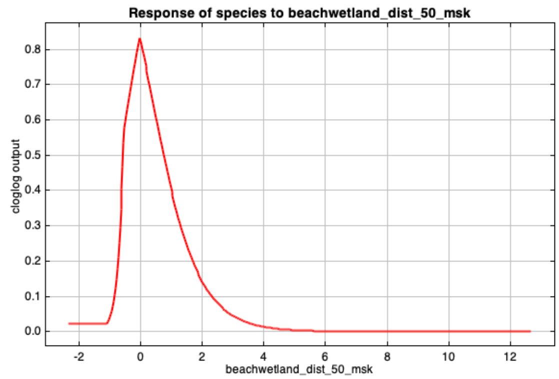
e. 

A3.4 a-e The top five contributing environmental variable response curves by permutation importance for HM (*k = 10*) roadkill risk model: a) managed bamboo forest, b) fruit trees, c) cistern, d) beach wetland, e) road width.

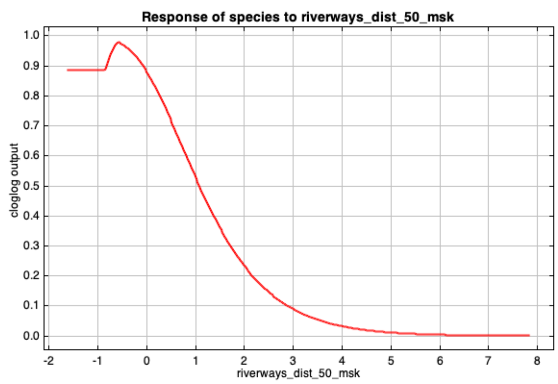

Response of species to manbamboo_focal_50_msk
cloglog output
manbamboo_focal_50_msk
a.


Response of species to buildings_focal_50_msk
cloglog output
buildings_focal_50_msk
b.


Response of species to fruittrees_focal_50_msk
cloglog output
fruittrees_focal_50_msk
c.

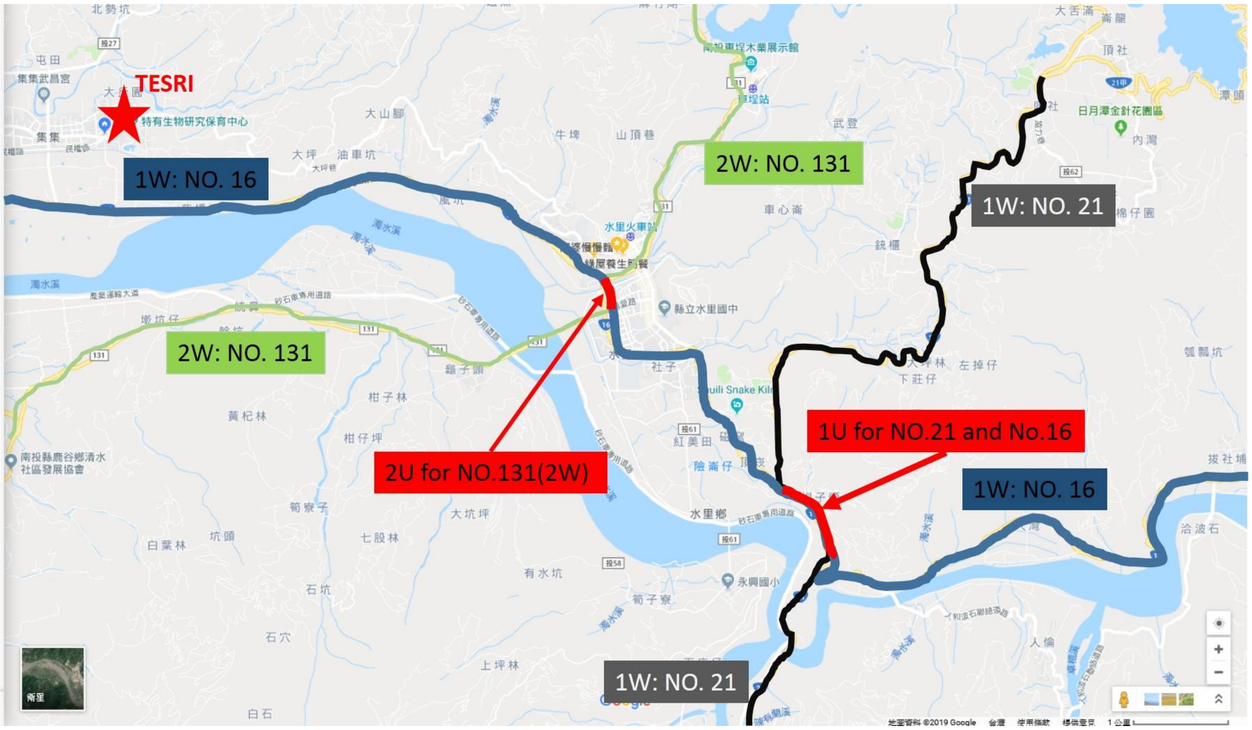


d.



e.

A3.5 a-e The top five contributing environmental variable response curves by permutation importance for HM (k = n) roadkill risk model: a) managed bamboo forest, b) buildings, c) fruit trees, d) beach wetland, e) riverways.



Appendix A4 An example of collinear roads in Taiwan. Collinear sections are in red.

Labels indicate road categories as described in Table 3.4.

APPENDIX B

Appendix B1 Predictive roadkill model interactive maps as .html files. All .html files can be found in the following GitHub repository (https://github.com/kmchyn/2019_TD_roadkill_risk). Each guild and species also have the .html file hosted as a website.

B1.1 Tasmanian devil (*Sarcophilus harisii*) interactive predictive roadkill model interactive map .html file can be found in the Github repository (https://github.com/kmchyn/2019_TD_roadkill_risk/blob/master/int_risk_map-01.html) and is hosted as a website (https://rawcdn.githack.com/kmchyn/2019_TD_roadkill_risk/2b8004e0be105d364d3ce5cc00dfb85e1ac688ae/int_risk_map-01.html)

User must zoom into Tasmania to view predictive devil roadkill risk model.