Impacts of land use and invasive species on native avifauna of Mo'orea, French Polynesia

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Oceanic islands are among the most endemically biodiverse ecosystems in the world. They have been adversely impacted by human expansion, which affects regional biodiversity by altering the natural habitats of vulnerable, indigenous species. Birds represent a valuable indicator species of environmental change due to their ability to adapt quickly. Investigating the relationship between environmental change, abundance, and behaviors of birds can help us better anticipate potential impacts to island ecosystems. In addition, we can understand the population trends and restricted ranges of native avifauna, identify the regions needing protection, and assess habitat vulnerability linked to anthropogenic activities. In Mo'orea, French Polynesia, we studied nine passerine bird species using automated acoustic recording devices placed in agricultural, forested, and mixed habitats. Based on call counts per unit time and occupancy modeling, we found evidence that three non-native species preferred agricultural areas and low-canopy cover over dense forested areas. Furthermore, native bird detectability and possibly abundance was significantly lower than non-native birds. Using hierarchical cluster analysis to support inferences regarding behavioral differences, we found that native bird calling activity was negatively associated with non-native bird calling activity. Altogether, these results suggest native bird populations are at risk in all of the habitats studied, but forests serve as a potential refuge.

1   Impacts of Land Use and Invasive Species on Native Avifauna of Mo'orea, French Polynesia
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12 **Abstract.**
13 Oceanic islands are among the most endemically biodiverse ecosystems in the world. They have
14 been adversely impacted by human expansion, which affects regional biodiversity by altering the
15 natural habitats of vulnerable, indigenous species. Birds represent a valuable indicator species of
16 environmental change due to their ability to adapt quickly. Investigating the relationship between
17 environmental change, abundance, and behaviors of birds can help us better anticipate potential
18 impacts to island ecosystems. In addition, we can understand the population trends and restricted
19 ranges of native avifauna, identify the regions needing protection, and assess habitat
20 vulnerability linked to anthropogenic activities. In Mo'orea, French Polynesia, we studied nine
21 passerine bird species using automated acoustic recording devices placed in agricultural,
22 forested, and mixed habitats. Based on call counts per unit time and occupancy modeling, we
23 found evidence that three non-native species preferred agricultural areas and low-canopy cover
24 over dense forested areas. Furthermore, native bird detectability and possibly abundance was
25 significantly lower than non-native birds. Using hierarchical cluster analysis to support
26 inferences regarding behavioral differences, we found that native bird calling activity was
27 negatively associated with non-native bird calling activity. Altogether, these results suggest
28 native bird populations are at risk in all of the habitats studied, but forests serve as a potential
29 refuge.

30
31 **Introduction.**
32 Biodiversity is impacted negatively by human-caused alterations of natural habitats through
33 industrialization, agriculture, logging, and commercial and residential development (Florens et
34 al., 2012; McKinney, 2002; Repetto,1988). The reduction in floristic and structural diversity
35 caused by agriculture can result in decreased habitat for many animals that rely on natural
36 ecosystems (Stoate et al., 2009). Agriculture practices specifically impact birds by altering and
37 eliminating their habitat, nesting availability, and food sources (Bunce et al., 1998; Vickery et
38 al., 2001). For example, the use of fertilizer is known to alter bird occurrence by changing the
39 amount and composition of soil-dwelling invertebrates for consumption (Scullion & Ramshaw,
40 1987; Tucker, 1992; Vickery et al., 2001). Livestock grazing can also alter biodiversity by
41 removing plants needed for nesting and shelter (McLaughlin & Mineau, 1995). Non-native
42 species may reduce biodiversity by encroaching and thriving on new, human-altered habitats
43 such as agricultural areas, and outcompeting their native counterparts for resources (Mack et al.,
44 2000; Gurevitch & Padilla, 2004).

45
46 Oceanic islands are among the most endemically biodiverse in the world because of their
47 isolation. It is their endemism that makes them vulnerable to anthropogenic disturbances (Paulay,
48 1994). French Polynesian oceanic islands host many native and endemic species from molluscs
49 *(Partula mooreana)* and plants *(Nesoluma nadeaudii)* to avifauna *(Ptilinopus purpuratus)*
50 (Clarke et al., 1984; Meyer & Butaud, 2009; Wray, 2013). On French Polynesian islands, the
51 need for human resources has led to more agriculture areas in recent years (Kennett et al., 2006).
52 When humans colonized French Polynesia in the early Holocene years, they introduced new
53 animals and plants, and altered the land so it could support their population's needs (Ferdon,
54 1981; Whistler, 1991). Agricultural intensity increased after the arrival of Europeans who
55 introduced pesticides and other agrochemicals (Bovis, 1976; Sakagawa, 1993).
56

57   Birds play a critical role in conservation, acting as "indicator" species as they adapt quickly to
58   environmental change demonstrating how other species may change in the future (Briggs et al.,
59   2013). By dispersing seeds, they keep the forests rich with plant growth and link habitats that
60   would otherwise remain unconnected (Galindo-Gonzalez et al., 2000; Didham et al., 2005). Bird-
61   related seed dispersal plays a major role in the genetic exchange in plant populations as well.
62   Should they disappear, birds would not perform ecosystem services, causing detriment to the
63   habitats they live in (Galindo-Ganzalez et al., 2000; Didham et al., 2005; Briggs et al., 2013).
64   Therefore, surveying birds to monitor changes in their distribution and population will help
65   researchers identify impact on the larger ecosystem (Briggs et al., 2013).
66
67   Despite agricultural conversion of native forests on the island of Mo'orea in French Polynesia,
68   little research has been conducted on the distribution of native and non-native avian fauna on this
69   island. Though the Opunohu Valley on Mo'orea was identified as an Important Bird Area (IBM)
70   by Birdlife International in 2006, a threat score, condition score, and action score have not yet
71   been assessed for the valley (BirdLife International, 2017). Therefore, the objective of the
72   present study was to survey nine passerine bird species across forested and agricultural habitats
73   within the Opunohu Valley using automated acoustic recording units. Two of the nine passerine
74   birds, the grey-green fruit dove and the Mo'orean kingfisher, are native (Wray, 2013), and
75   Mo'orean kingfisher is an endemic to Mo'orea (Wray, 2013). Automated acoustic recording
76   units are a valuable technology to help survey a wide variety of avian species concurrently
77   (Haselmayer & Quinn, 2000; Hobson et al., 2002; Rempel et al., 2005; Brandes, 2008; Furnas &
78   Callas, 2015).
79
80   Based on the survey, we evaluate differences in activity and occupancy among native and non-
81   native species, attempt to assess their vulnerabilities to agriculture and loss of forest habitat, and
82   also make recommendations for expanding avian monitoring throughout Mo'orea.
83
84   **Methods.**
85   *Study area*
86   We conducted this research on the island of Moorea, a high volcanic island, 134 km^2
87   in size, in the Society Islands of French Polynesia (Fig 1, 2), where human settlement occurred
88   heavily along the coast of the island as well as in flat river valleys. However, much of the
89   island's rugged interior is unsettled and covered in dense forest filled with Tahitian chestnut
90   *(Inocarput fagifer)*, hibiscus *(Hibiscus rosa-sinensis),* miconia (Miconia calvescens), and
91   candlenut *(Aleurites moluccana*). Our bird surveys were limited to the Opunohu Valley, a fertile
92   river valley of diverse land use, from intensive agriculture to protected forests, both interspersed
93   among mixed-used areas. Much of the Opunohu Valley floor currently provides livestock
94   grazing whereas the remnant lowland valley forests are dominated by dense vegetation, some of
95   which is non-native (Lepofsky et al., 1996). Farming is intermixed within the Opunohu Valley in
96   multiple areas (HOW MANY AREAS).
97
98   *Study Species*
99   The native birds we targeted for acoustic surveys are grey-green fruit dove (*Ptilinopus
100 purpuratus*) and Mo'orean kingfisher (*Todiramphus veneratus*). The introduced, resident
101 avifauna species we surveyed are red jungle fowl (*Gallus gallus*), zebra dove (*Geopelia striata*),
102 red-vented bulbul (*Pycnonotus cafer*), common myna (*Acridotheres tristis*), silvereye (*Zosterops

103   *lateralis*), common waxbill (*Estrilda astrild*), and red-browed firetail (*Neochmia temporalis*).
104   Together, these nine species represent all of the terrestrial passerine avifauna on Mo'orea,
105   excluding chestnut-breasted mannikin (*Lonchura castaneothorax*) (Wray, 2013). We were not
106   able to distinguish Chestnut-breasted mannikin (*Lonchura castaneothorax*), a terrestrial resident
107   passerine, from spectrogram displays, or find evidence of it being in the agricultural or forested
108   areas so it was not included in this study. Additionally, the Tahiti swiftlet (*Aerodramus*
109   *leucophaeus)* has not been seen on Mo'orea since 1973 (Marshall Cavendish Corporation, 2001).
110   We did not verify the presence of this species during monitoring so it was also excluded in this
111   study. We did not include seabirds or shorebirds in our study because they were rarely
112   encountered at the sites we sampled in the Opunohu Valley.
113
114   *Selection of field sites*
115   To assess the impact of human land use on the bird community, we first stratified the study area
116   by land-use types (forested, agricultural, or mixed) based on visual inspection of satellite
117   imagery (Google Earth). We overlaid a grid consisting of 267 m wide quadrats and assigned each
118   to one of the three strata. Second, we randomly selected five quadrats within each of the three
119   land use types (15 sites total, Fig 1). We constrained randomization so that each study site was
120   located >250 m apart to ensure double counting did not occur (Bibby et al., 2000). We examined
121   each site in person before sampling to ensure that the habitat type was identified correctly from
122   the satellite imagery.
123
124   Ideally, we established a survey site at the center of a selected quadrat. If this point was not
125   accessible, a random distance and bearing was chosen to offset the location. We recorded canopy
126   cover by using five descriptive canopy cover types: open, open/moderate, moderate,
127   moderate/covered, and covered. Canopy cover was defined by visually assessing the percent of
128   canopy covered by vegetation within an approximately 10 meter by 10 meter box. 0% coverage
129   defined open canopy, 25% coverage defined open/moderate canopy, 50% coverage defined
130   moderate canopy, 75% coverage defined moderate/covered canopy, and 100% coverage defined
131   covered canopy.
132
133   *Acoustic sampling*
134   We deployed an automated acoustic recording unit [Olympus DM-620s (Olympus Corporation,
135   Center Valley, PA) or Songmeter4 (Wildlife Acoustics Inc., Concorde, MA, USA)] to record
136   bird vocalizations at each survey site. We rotated use of the two models of recording devices so
137   that an equal number of samples from each model were made in each habitat stratum. This
138   helped us mitigate any issues pertaining to an expected difference in effective sampling area of
139   the two models. The detection range of the acoustic recorders was not measured in our study.
140   However, after attempting visual surveys, we discovered that acoustic recorders in all forested
141   areas and many mixed areas were able to receive calls from birds that were visually obstructed
142   from extremely dense vegetation. For less dense forested habitats in California, Furnas and
143   Callas (2015) determined an effective acoustic range of approximately 50 m for the Olympus
144   recorders. It is likely that the detection range of the Wildlife Acoustics recorder is greater than
145   that of the Olympus.
146
147   Each automated recorder was placed on the ground within 5 m of the selected point in the
148   quadrat where reception of song was likely to be highest. Adjacent sites were not sampled on the

149 same day to further reduce the chance of recording the same individual from two different sites.
150 In forested sites, we placed the recording device in the clearest area within the 5 m radius so
151 acoustic reception would not be altered by understory vegetation. Following the protocol of
152 Furnas and Callas (2015), we programmed the units to record for five minutes three times each
153 morning commencing at 30 minutes before local sunrise, sunrise, and 30 minutes after sunrise.
154 Surveys were repeated on three consecutive mornings totaling nine recordings summing to 45
155 minutes at each site. We chose this method to ensure that all species of birds were recorded,
156 taking into account that species may prefer different calling hours. The recordings from our 15
157 survey sites summed to 675 minutes from 45 site-morning combinations. The acoustic recorders
158 were set to record at a sample rate of 24 kHz and a reception level minimum of 16.0 dB and a
159 maximum of 122 dB. The bandwidth of the recording devices ranged from 20 Hz to 49 kHz.
160
161 *Call validation and interpretation of survey recordings*
162 To ensure accurate interpretation of our survey recordings, we first completed a pilot study to
163 record reference bird calls for each species while visually confirming the species identities of the
164 vocalizing birds. Multiple reference examples were made for each species to ensure variety in
165 call types identified. We made spectrograms of the validated calls and used them to calibrate
166 species identifications in spectrograms of the recordings from the field.
167
168 We extracted the acoustic data from our recording devices via a micro SD card and uploaded
169 them to a computer. All acoustic recordings were converted into an adapted .wav file format for
170 analysis. Analyses were conducted using the Triton processing software program (Wiggins &
171 Hildebrand, 2007), based in MATLAB (MathWorks Inc., Natick, MA), to calculate and display
172 standard spectrograms, to perform audio playbacks, and to log call detections.
173
174 One trained acoustic analyst interpreted all of the recordings to minimize any bias that might
175 occur with multiple analysts. The analyst excluded any detections in which she was unsure of the
176 species identification. Less than 20 vocalizations were excluded. We excluded two out of the 45
177 site-mornings because of intense anthropogenic noise covering birdcalls in the spectrograms.
178
179 The analyst visually scanned spectrograms by examining a 10 second window with time and
180 frequency resolutions bins of 5 seconds and 100 Hz respectively (1000 point FFT, 75% overlap).
181 Because of the differences in call structure, defining a single vocalization differed for each
182 species as described below.
183
184 Red-vented bulbul calls are most commonly two or three toned, and range from frequencies of
185 1000 to 3000 hz. Red-vented bulbuls are less commonly found making single tone calls
186 (Supplemental Information). Every every two-tone and three-tone call was considered unique
187 (recorded as a new call) (Supplemental Information). A unique call could be from the same
188 individual, or a new individual. Common waxbill darts are categorized by their high frequency
189 and short duration. The darts range in frequency from 3000 to 8000 hz. The source level is low,
190 and is sometimes, but not often, covered by the high source level of the silvereye call
191 (Supplemental Information). Every dart was considered unique. Zebra dove, like grey-green fruit
192 dove, show a call that contains a train of coos. The coos are faster and of shorter duration than
193 the grey-green fruit dove. Zebra dove coos are also at a higher frequency than grey-green fruit
194 dove, at approximately 1000 to 15000 hz (Supplemental Information). Zebra dove calls are

195 considered unique every time a signature large coo occurs at the beginning of the "coo train."
196 The red jungle fowl call is a combination of sweeps and screeches, varying in frequency, and
197 most commonly found in between 1000 and 4000 hz (Supplemental Information). Every screech
198 was considered a new call. The grey-green fruit dove "coo-train" is low frequency, and varied in
199 duration at approximately 400 hz (Supplemental Information). The large "coo" at the beginning
200 of the grey-green fruit dove "coo train" determined the beginning a new call. The Mo'orean
201 kingfisher call is categorized as a shuddering "klew" that can vary greatly in duration. The
202 signature shudder of this call was was the largest identification factor. The frequency range of
203 the Mo'orean kingfisher call was very large, at times ranging from 10 to 4000 hz in one call
204 (Supplemental Information). The Mo'orean kingfisher call was considered unique if there was a
205 two-second gap between the shuddering "klews." The common myna call was very complex, and
206 was comprised of different trills, screeches, downsweeps, and tonal calls. The common myna,
207 like the Mo'orean kingfisher, has a large range of frequency-calling abilities, and can range from
208 1000 to 8000 hz (Supplemental Information). The common myna call was considered new if
209 there was a one second gap between the calls. The red-browed firetail call is noted as a high
210 frequency upsweep trill. The upsweep is consistently most intense at a frequency of 6000 to 8000
211 hz (Supplemental Information). Each upsweep made was a new call. The downsweep of the
212 silvereye is most commonly found at a frequency of 3000 to 5000 hz (Supplemental Information)
213 and its song is made up of an entanglement of downsweeps at this frequency. Every silvereye
214 downsweep was considered its own call, including all of the downsweeps making up the song.
215 Because of the wide variety of frequency, duration, and call structure in the different species'
216 calls, disentanglement of calls was not an issue in the spectrogram analyses.
217
218 *Statistical Analyses*
219 We used nested ANOVA to evaluate differences in call count per unit time in different habitats
220 for each species. To this we tallied the number of calls heard per 5-minute survey by habitat and
221 species. We tested if there were any significant differences in mean counts among the habitats
222 by species.
223
224 We used hierarchical cluster analysis to further elucidate patterns of co-detection of bird species
225 (Sharma, 1996; McCune et al., 2002). We limited this analysis to the subset of five sites at which
226 all nine avian species were detected, a constraint which permitted inferences about temporal
227 partitioning of vocal behavior among native versus non-native species. We used logistic
228 regression to confirm temporal difference in species detections.
229
230 *Occupancy Modeling*
231 Occupancy modeling allowed us to differentiate our data on the species' calling frequencies into
232 separate processes governing the proportion of sites occupied by a species versus the detection
233 probability of a species at an occupied site (MacKenzie et al., 2006). We used a multi-species
234 modeling approach (Tingley et al., 2012; Iknayan et al., 2014) because of the small sample size.
235 We had an insufficient sample size to include covariates on occupancy, but we did include
236 canopy cover and whether a survey occurred before, during, or after sunrise as covariates on
237 detection probability. We used the canopy cover covariate as a proxy representing the different
238 land use types we surveyed (agricultural, mixed, and forest), because canopy cover was generally
239 higher at forested and non-agricultural sites. We also used detection probability as an indicator of

240 abundance, by reasoning that a species was more detectable at an occupied site because multiple
241 vocalizing individuals were present (Royle & Nichols, 2003).
242
243 Our model included fixed effects on species occupancy and hyperparameters on all detection
244 probability parameters. Because we only surveyed focal species, we did not use data
245 augmentation in the model. We fit a Bayesian model solved using a Markov Chain Monte Carlo
246 (MCMC) algorithm (Link et al., 2002) implemented in JAGS (4.2.0, Plummer 2003) accessed
247 via R statistical software (3.3.1, www.r-project.org) with the jagsUI package (Kellner, 2015).
248 Uninformative priors were assumed for all parameters. Three independent chains of 10,000
249 samples were run with a burn-in period of 5000 and a thinning rate of three. Effective mixing of
250 these chains was assessed visually and by means of the Gelman-Rubin convergence statistic
251 (<1.1;Gelman et al., 2004).
252
253 **Results.**
254 *Results for Average Calling Number*
255 The average number of calls per 5-minute survey was highest for two introduced species,
256 silvereye and red-vented bulbul (Table 1). It was lowest for the two native species, Grey-green
257 fruit dove and Mo'orean kingfisher. Common waxbill, zebra dove, and common myna all
258 showed a significantly greater average call number per 5-minute survey in the agricultural sites
259 ($p < 0.01$) whereas red jungle fowl was significantly more prominent in forested areas ($p < 0.05$)
260 (Table 1). Red-vented bulbul, red jungle fowl, silvereye, red-browed firetail, Mo'orean
261 kingfisher, and grey-green fruit dove showed no significant habitat association with the average
262 number of calls data (Table 1). Zebra dove, common myna, and common waxbill showed a
263 significant association with agricultural areas based on the number of total average calls at each
264 site per 5 minutes (Table 1).
265
266 *Hierarchal Clustering Results*
267 We found strong evidence of temporal partitioning in the vocalizations of native versus non-
268 native species. In the assessment of 5-minute surveys, the hierarchical cluster analysis split
269 detected species into two distinct groups that completely coincided with native versus non-native
270 species (Fig 3). For Mo'orean kingfisher, logistic regression confirmed its detection during a
271 survey was negatively associated ($p = 0.016$) with the total number of non-native birds detected
272 concurrently. On the other hand, there was no evidence of avoidance among the two native birds
273 ($p = 0.444$)
274
275 *Occupancy Modeling Results*
276 All but one of the species had occupancies >0.8, suggesting that these species were widespread
277 throughout the study area (Fig 4). Only grey-green fruit dove, a native species, had an estimate
278 occupancy of <0.8, but it was still >0.6.
279
280 Different morning times explained differences in detection probability among non-native species
281 (Fig 5). All non-native species, except red-vented bulbul and red jungle fowl, displayed the same
282 pattern whereby detection probability was higher after sunrise compared to before sunrise. In
283 contrast, there was no discernable temporal pattern for the two native species; they did not call
284 more or less at any of the morning times studied.
285

286 We identified a negative relationship between canopy cover and detection probability for three
287 non-native species (common myna, common waxbill, and zebra dove), suggesting that these
288 species may be more abundant in agricultural habitats (Fig 6). Four non-native species (red-
289 vented bulbul, red jungle fowl, silvereye, zebra dove) had the highest average detection
290 probabilities per survey (>0.5), whereas both native species (grey-green fruit dove and Mo'orean
291 kingfisher) were among the group with the lowest detection probabilities (<0.5) (Fig 5). Taken
292 together, the occupancy modeling findings suggest that, although widely distributed, native
293 species may occur at lower levels of local abundance than non-native species.
294
295 **Discussion.**
296 *Acoustic Monitoring*
297 Automated acoustic recording devices have been used in many different fields of biology to note
298 acoustic activity of various species during different times of the year as well as different times of
299 the day (Jones et al., 2013; Baumann-Pickering et al., 2015). These monitoring devices allowed
300 us to efficiently repeat surveys at sites in remote areas that were difficult to access due to dense
301 vegetation and steep inclines (Frommolt et al., 2008). However, visual point counts in addition to
302 acoustic recordings could be conducted in Mo'orea to further improve the accuracy and precision
303 of our surveys (Bibby et al., 2000). Both sources of data could be included in the same
304 occupancy model (McGrann & Furnas 2016).
305
306 *Inference about activity and abundance*
307 In this study, we found non-native birds calling at a significantly greater rate than native birds in
308 each of the three habitats studied. Female and male avifauna in the tropics are known to call
309 year-round; however, calling activity and call repertoire may change during breeding season
310 (Montgomerie & Weatherhead, 1988; NE Langmore, 1998). The breeding seasons of the native
311 and non-native avifauna on Mo'orea vary from species to species or are unknown entirely
312 (Spotswood, 2011). Future studies should analyze if and when the calling activity of Mo'orean
313 avifauna changes throughout breeding seasons.
314
315 Furthermore, our use of occupancy modeling helped us make inferences about occupancy and
316 abundance for native and non-native species. Survey-level detection probability was lowest for
317 the two native species, grey-green fruit dove and Mo'orean kingfisher. This difference suggests
318 that, while all bird species were widely distributed across all three land-use types (agricultural,
319 forested, and mixed), local abundance of native species may have been lower than non-native
320 species at occupied sites. On the other hand, detection probability of three non-native species
321 (zebra dove, common myna, and common waxbill) was significantly higher in low canopy
322 habitats, suggesting higher abundances in agricultural areas. This pattern may allow forested
323 areas to provide a refuge for the native species because of reduced use of these are by non-
324 natives.
325
326 One caveat that must be considered when linking detection probability to inferences about
327 abundance (Royle & Nichols, 2003) is the sound transmission properties of different habitats.
328 Lower detectability of three exotic species in higher canopy cover could be partially due to
329 greater attenuation of calls in forested habitats (Catchpole & Slater 2008). Low detectability of
330 native birds due to sound attenuation, however, is unlikely. The call structure of native birds
331 provides a greater likelihood of transmission because of the low frequency call of grey-green

332 fruit dove and the high intensity, long duration call of Mo'orean kingfisher. Low frequency calls
333 are more likely to travel through forest habitats (Catchpole & Slater, 2008), which may be a clue
334 to the evolutionary and behavioral adaptations of the native birds being adapted to live in a high-
335 density forest area. Therefore, lower detection probabilities of native versus exotic birds may be
336 evidence to reduced abundances for the former.
337
338 *Inferences about behavior*
339 The results of hierarchical cluster analysis and logistic regression showed that Mo'orean
340 kingfisher calling behavior was negatively associated with the presence of non-native calls.
341 Mo'orean kingfisher calls lie in the same frequency band as all of the non-native species' calls.
342 Mo'orean kingfisher calls could be obfuscated by the vast number of calls from the non-native
343 birds (as high as 40 per minute for red-vented bulbul). Mo'orean kingfisher may not be calling as
344 frequently because their songs are not effectively transmitted in the presence of the non-native
345 calls, or because there is a lower density of Mo'orean kingfisher altogether. The obfuscation of
346 the Mo'orean kingfisher call may adversely affect their social behavior, reproductive success,
347 and overall population numbers.
348
349 Native bird calls may be less obfuscated by non-natives in the early morning. As seen in the
350 morning time detectability results, native species showed no significant difference in calling
351 times before and after sunrise, while non-native species were detected primarily after sunrise.
352 Native passerines in Mo'orean perhaps avoid competition with non-natives by calling before
353 sunrise when there is less non-native activity and less obfuscation of native calls. This result
354 agrees with the notion of non-native species displacing native species from their behavioral
355 niches (Mooney & Hobbs, 2000), in this case in terms of acoustic transmission.
356
357 Additional studies should be conducted to look into the morning calling times of native birds in
358 areas where there are no non-native birds present, compared to areas with a loud non-native bird
359 chorus to verify if natives are avoiding the non-native chorus. In addition, birds may be active in
360 calling at dusk as well as dawn (Zwart et al., 2014). Calling patterns prior to dusk should be
361 investigated to see if there is a different calling pattern for non-native and natives in the late
362 afternoon.
363
364 *Ecology of non-native and native avifauna*
365 The results of the present study demonstrate that non-native bird species thrive in all of the tested
366 habitats consistent with prior studies showing non-natives prospering in disrupted habitats (Mack
367 et al., 2000; Gurevitch & Padilla, 2004). The non-native common myna was significantly more
368 active in the habitats disrupted by agricultural expansion. Interestingly, common myna removal
369 projects have been initiated in the forests of Mo'orea's neighbor island, Tahiti, to protect native
370 species (BirdLife International, 2016). Common myna removal projects may prove to be more
371 effective if conducted in agricultural areas as well as forests, based on our findings that common
372 mynas were less frequently detected in forests.
373
374 There is very little information about the habitat requirements, calling activity, and natural
375 history of native avifauna in French Polynesia (Coulombe et al., 2011). Mo'orean kingfishers
376 were shown in this study to have low call counts, low detection probability, and a negative
377 correlation with non-native calling activity in all of the habitats studied. Future research should

378 analyze habitat preferences of Mo'orean kingfishers in greater detail. Closely related kingfisher
379 species have been seen habituating coconut trees in managed and unmanaged coconut farms
380 (Coulombe et al. 2001). Studies of the Mo'orean kingfisher should be conducted in coconut
381 farms to support or refute this idea.
382
383 Grey-green fruit dove exhibited low calling activity, lower occupancy than other species, and
384 low detection probabilities in all habitats studied. Grey-green fruit doves were more active in
385 mixed habitats with moderate canopy cover; however, the differences were insignificant.
386 Different canopy cover and habitats should be analyzed to see what the preferential habitat is for
387 grey-green fruit dove so population restoration can be put into action.
388
389 *Conclusion*
390 Multi-species occupancy modeling and automated acoustic recording devices are tools that could
391 be used to increase the precision of parameter estimation for testing habitat and behavioral
392 hypotheses. We applied them to provide the first comprehensive evaluation of avifauna on
393 Mo'orea. Altogether our findings suggest that native species are avoiding calling when non-
394 natives are active and that abundances of natives may be substantially lower than of non-natives.
395 Forest may provide a refuge for native species because non-natives were detected less frequently
396 there. However, the conclusions of our study are limited by a small sample size. We recommend
397 additional sampling using our methods as well as point counts. Additional surveys are necessary
398 to create a clearer picture of the habitat preferences Mo'orean kingfishers and grey-green fruit
399 doves and the interactions of these species with non-native avifauna. This information will be
400 essential for planning conservation actions protecting native birds in French Polynesia from
401 endangerment or extinction.
402

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Figure 1

Map of Mo'orea with sampling sites

Sampling sites in the Opunohu Valley of Mo'orea. Black squares indicate forest sites. Gray circles are mixed-covered sites. White triangles are agricultural sites.

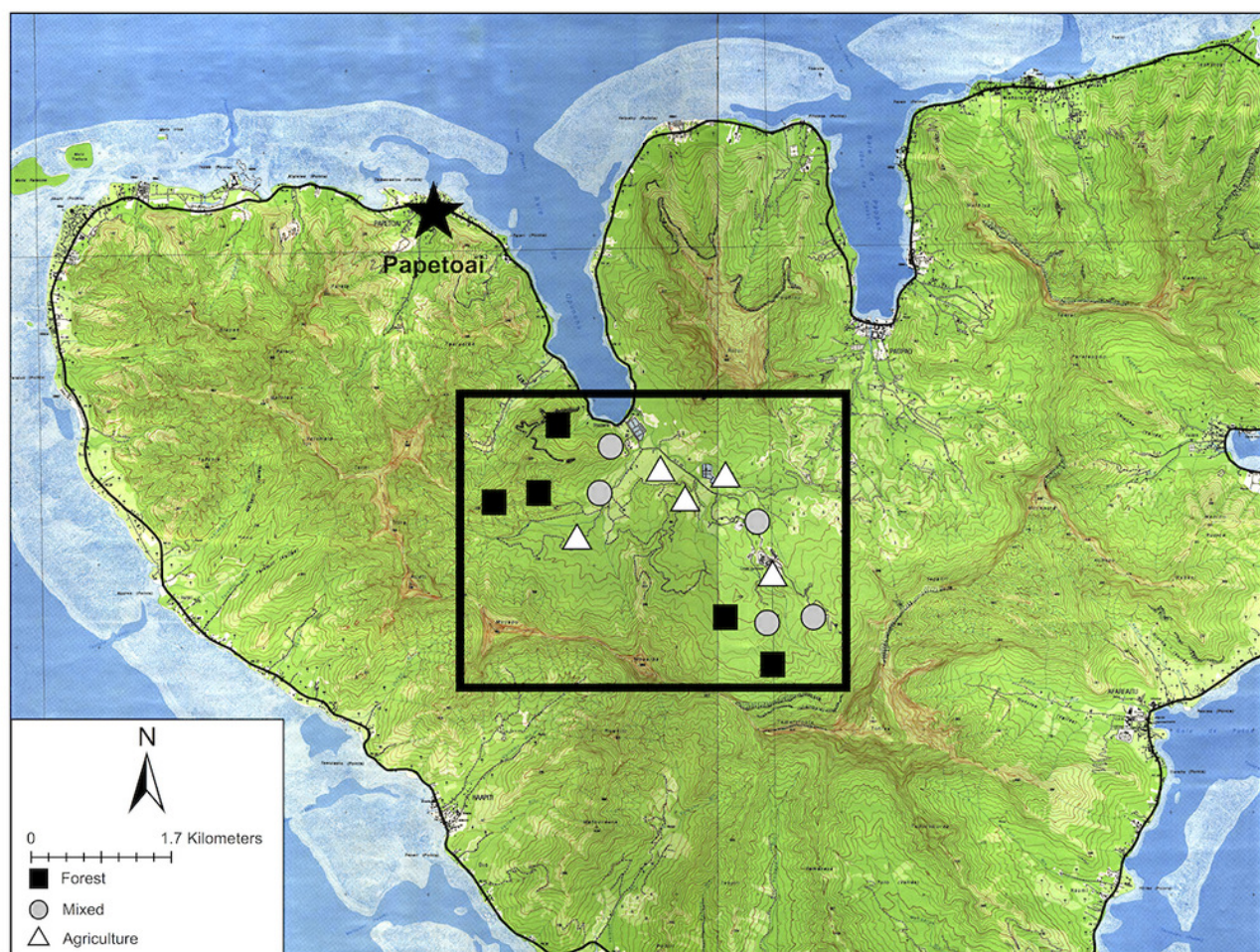
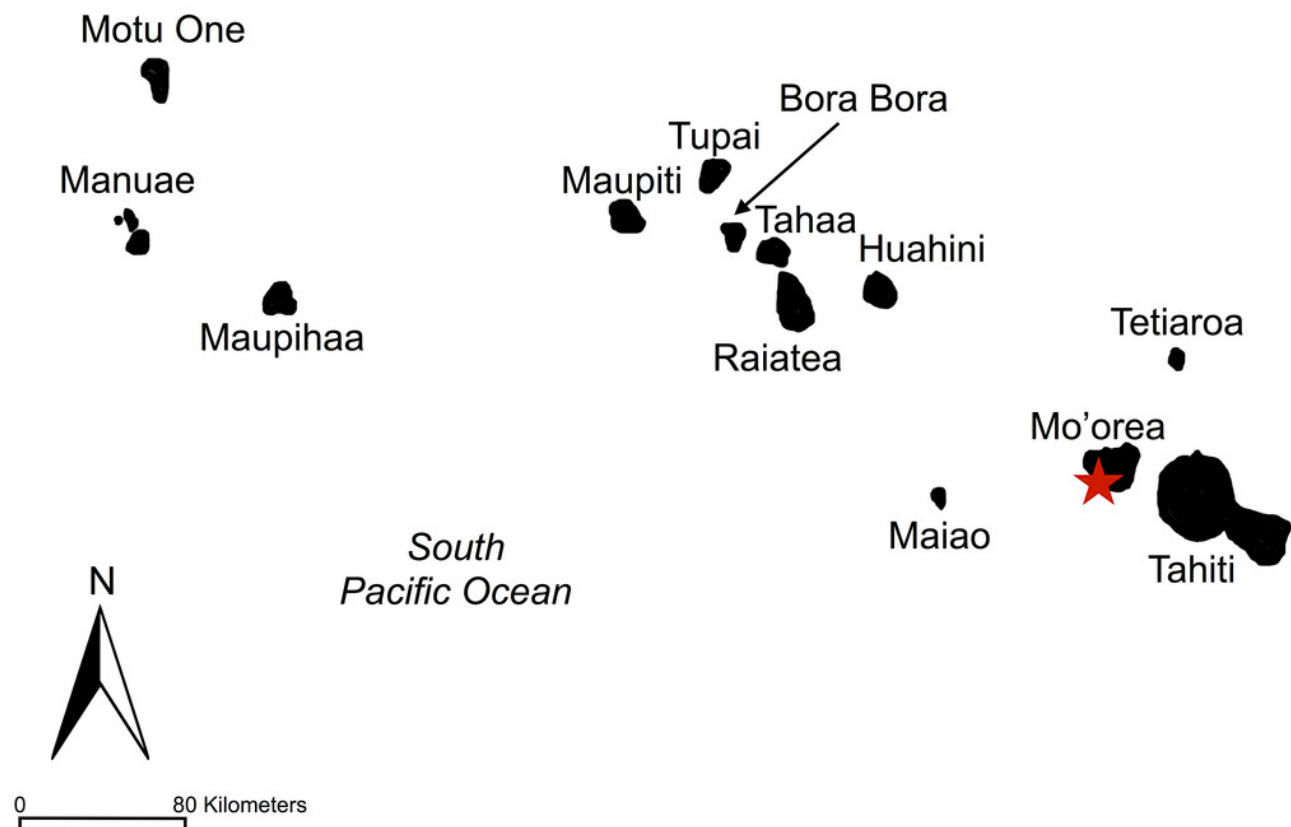



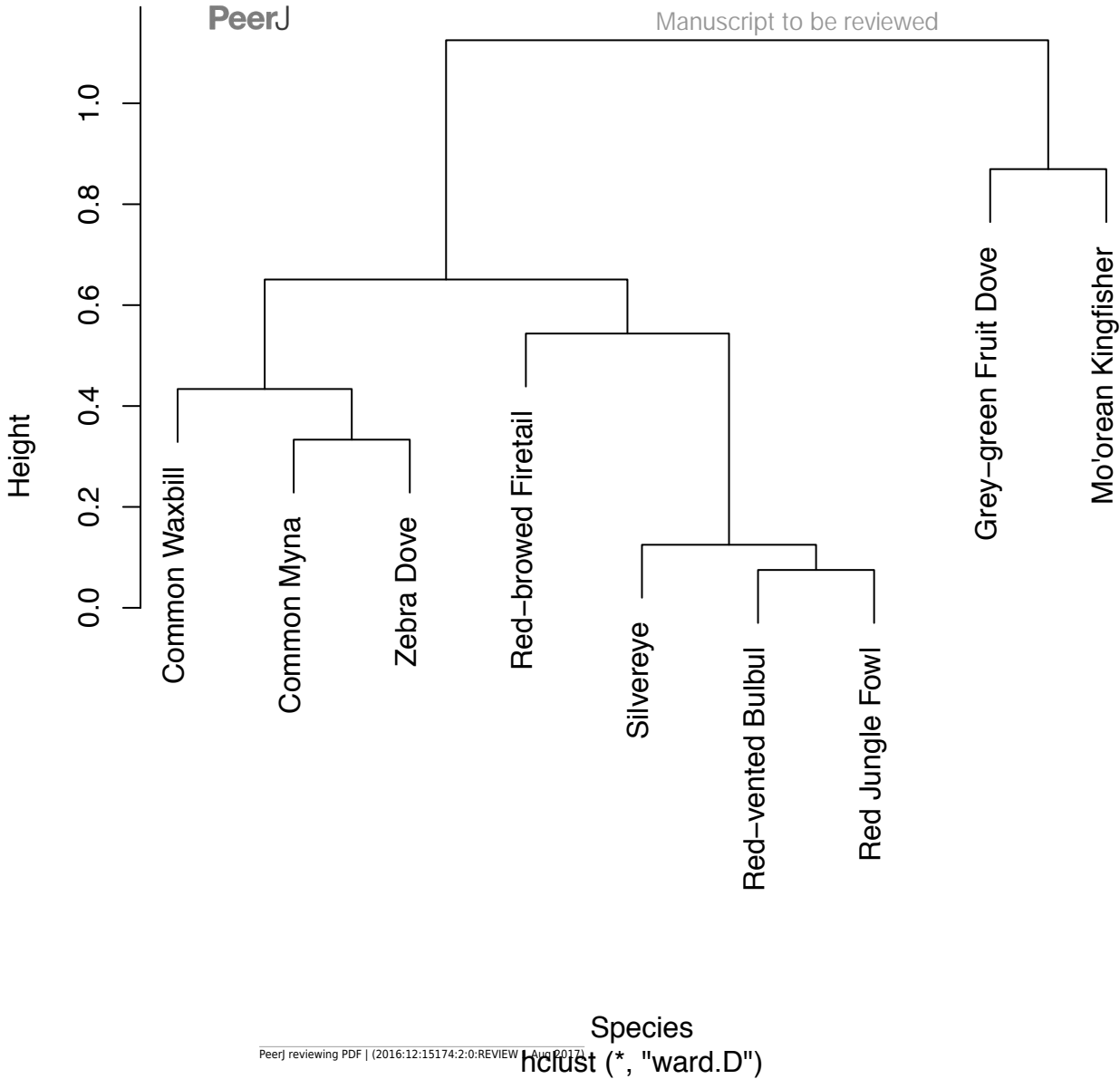
Figure 2

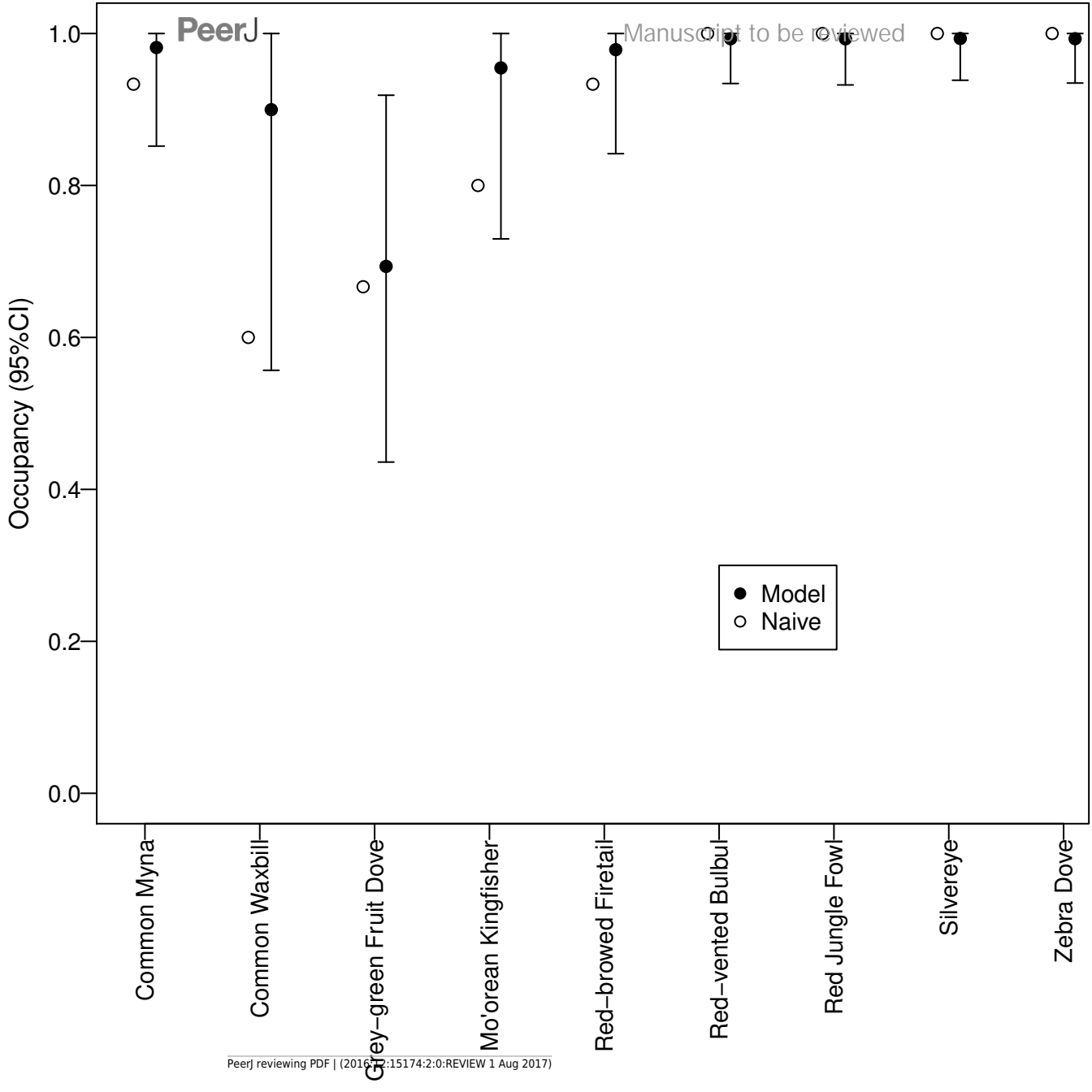
Map of Society Islands

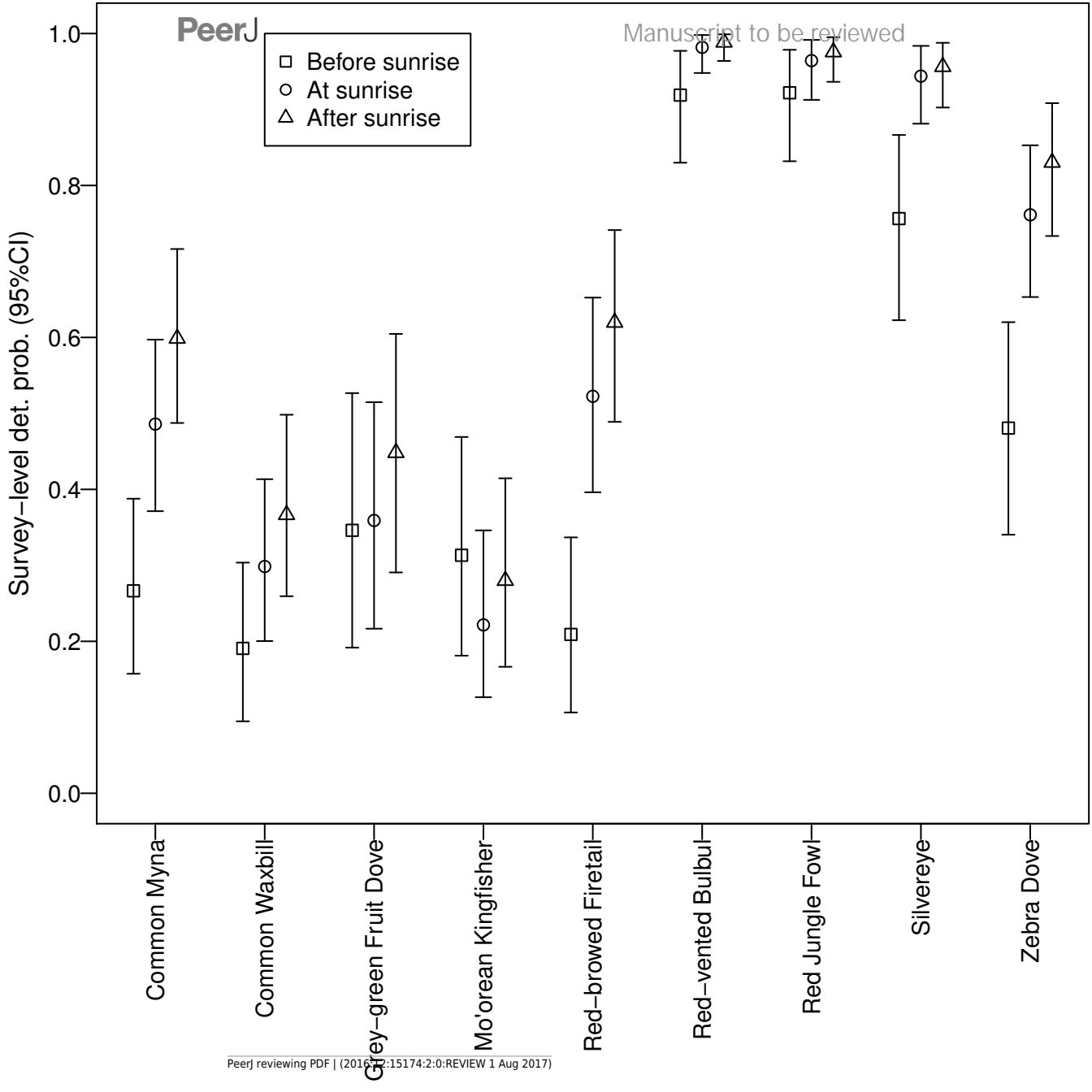
Society islands including Tahiti, Mo'orea, Tetiaroa, Maiao, Huahini, Raiatea, Tahaa, Bora Bora, Tupai, Maupiti, Maupihaa, Manuae, and Motu One. The island sampled, Mo'orea, is marked by a red star.

Hierarchical clustering of co-detection of nine bird species from five sites

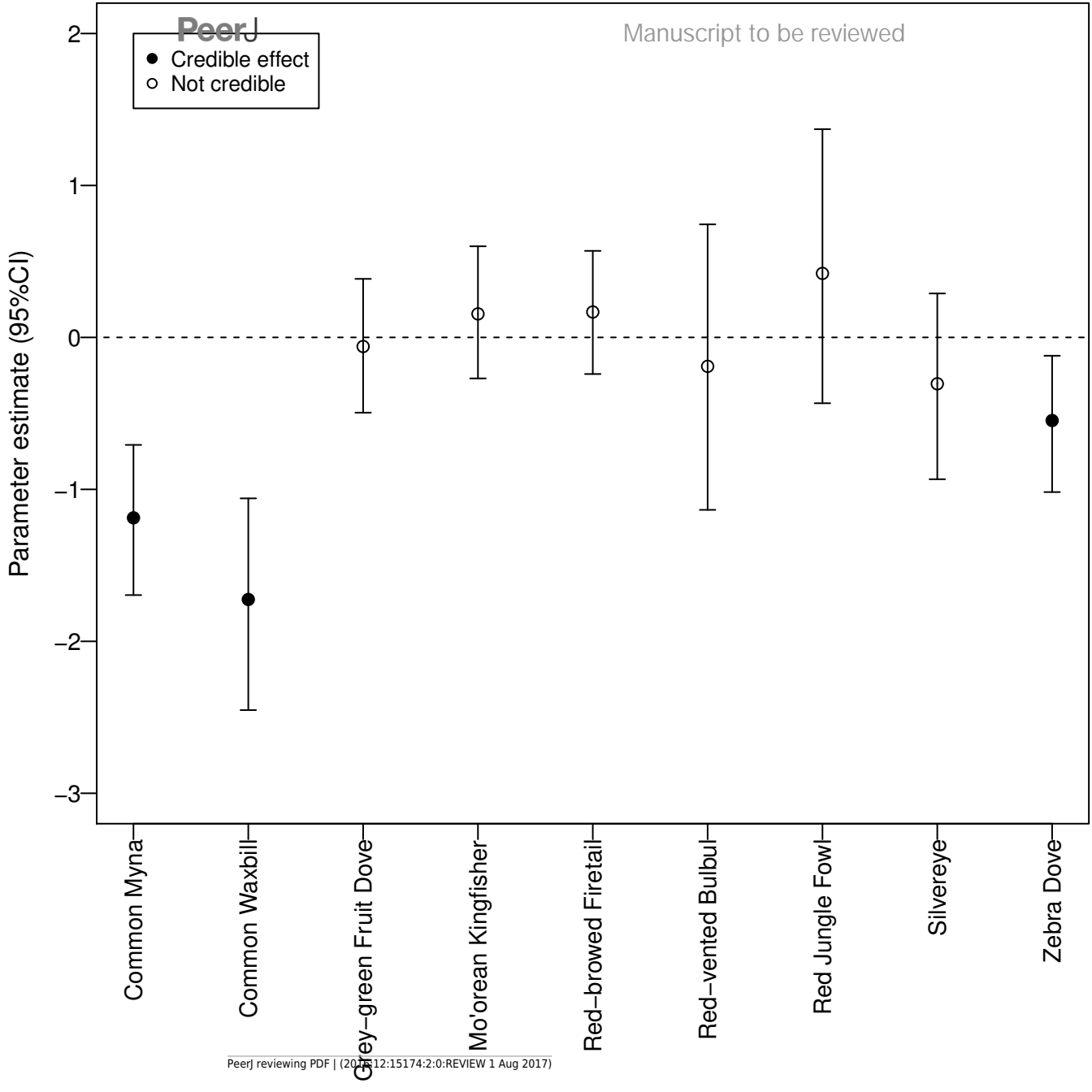
Hierarchical clustering was limited to the five sites at which all nine bird species were present. Temporal partitioning and vocal behavior of the nine birds are presented with this clustering.

Species

hclust (*, "ward.D")

Estimated occupancy

Estimated occupancies of avian species surveyed using automated recorders. A multispecies occupancy model was used to address potential bias due to detection probabilities <1. Naive occupancy is the proportion of survey sites at which a species was detected.

Canopy cover detection probability

Associations between forest canopy cover and detection probability for avian species surveyed using automated recorders. We deemed there to be an association when the credible interval for the parameter estimate did not overlap zero.

Estimated detection probabilities

Estimated detection probabilities of of avian species surveyed using automated recorders. Surveys were 5 minutes once a day repeated over 3 consecutive days commencing 30 minutes before sunrise, at sunrise, and 30 minutes after sunrise.

The effect of habitat association on number of calls

Mean call number for all three habitats including the standard error (SE). F-value, and P-value for all habitats. For all species, df total was 103, df factors was 2, and df error was 101.

	Mean Call Number Agriculture ± SE (# Calls)	Mean Call Number Forest ± SE (# Calls)	Mean Call Number Mixed ± SE (# Calls)	F-value	Agriculture-Forest P-value	Agriculture-Mixed P-value	Forest-Mixed P-value
Red-vented Bulbul	202.30 ± 28.98	141.78 ± 19.76	101.58 + 12.99	5.21	0.13	0.01	0.42
Red Jungle Fowl	34.14 ± 4.76	51.92 ± 6.45	29.33 ± 4.51	4.93	0.05	0.80	0.01
Zebra Dove	44.73 ± 7.81	4.58 ± 1.41	21.45 ± 5.07	13.79	0.00	0.01	0.09
Common Myna	20.57 ± 4.25	1.06 ± 0.46	3.00 ± 1.58	16.01	0.00	0.00	0.87
Silvereye	272.62 ± 37.07	269.97 ± 43.46	175.82 ± 27.63	2.13	1.00	0.16	0.18
Common Waxbill	41.05 ± 11.72	0.17 ± 0.17	0.52 ± 0.25	11.23	0.00	0.00	1.00
Red-browed Firetail	1.97 ± 0.68	4.58 ± 1.80	5.21 ± 1.87	1.30	0.44	0.30	0.96
Mo'orean Kingfisher	0.54 ± 0.19	0.58 ± 0.22	0.48 ± 0.32	0.04	0.99	0.99	0.96
Grey-green Fruit Dove	0.27 ± 0.11	0.44 ± 0.12	0.48 ± 0.15	0.85	0.58	0.45	0.97

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