



Nutrient subsidy indicators predict the presence of an avian mobile-link species



Christina A. Buelow^{a,b,*}, Ronald Baker^{a,b}, April E. Reside^c, Marcus Sheaves^{a,b}

^a College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

^b TropWATER, Centre for Tropical Water & Aquatic Ecosystem Research, James Cook University, Townsville, QLD 4811, Australia

^c Centre for Biodiversity and Conservation Science, The University of Queensland, St Lucia, QLD 4072, Australia

ARTICLE INFO

Keywords:

Nutrient subsidy
Connectivity
Stable isotopes
Migration
Ecosystem function
Stoichiometry

ABSTRACT

Island ecosystems can be inordinately dependent on avian nutrient subsidies because of their isolation from external nutrient pools. We investigated relationships between several nutrient subsidy indicators and the presence of Torresian Imperial-Pigeon (TIP, *Ducula spilorrhoa*) breeding colonies in island forests of northeast Australia. The following nutrient subsidy indicators were measured in island forest soil and leaf samples: nutrient origin (δN^{15} and δC^{13}); total carbon (C), nitrogen (N), and phosphorus (P) levels; and nutrient quality (C:N:P ratios). Random Forest models were used to determine the relative importance of nutrient subsidy indicators for classifying island forests as 'TIP colony present' or 'TIP colony absent'. Total P was the most important soil nutrient subsidy indicator, while δN^{15} was the most important leaf nutrient subsidy indicator. Furthermore, in both soil and leaves, δN^{15} enrichment and N and P levels increased as the probability of TIP colony presence increased. Measures of nutrient quality also implied plant growth rates were higher in island forests with increased likelihood of TIP colony presence. Torresian Imperial-Pigeons should be classified as an avian mobile-link species with an important role in island ecosystem functioning, encouraging further investigation of the direct and indirect effects associated with TIP nutrient subsidies. This research highlights the importance of understanding the local-scale connectivity processes that underpin the longer distance movements of inter-continental migrants for effective ecosystem management.

1. Introduction

Ecosystem resilience is defined as the ability to withstand perturbation and is dependent on myriad factors, such as nutrient availability (Holling, 1973; Gunderson, 2000). Nutrient availability directly influences ecosystem productivity, and *in situ* nutrient production is often supplemented by subsidies from other ecosystems through transport by wind, water, or mobile organisms (Polis et al., 1997). Island ecosystems are relatively isolated from other landmasses, meaning that external nutrient subsidies provided by mobile organisms may play a critical role in their functioning and resilience. Information regarding the origin, quantity, and quality of island nutrient subsidies is needed to evaluate the importance of mobile link species for island ecosystem functioning.

Due to their high mobility and colonial roosting or nesting behaviour, seabirds are key vectors in the transportation of marine-derived nutrients to island ecosystems (Lundberg and Moberg, 2003; Ellis,

2005; Sekercioglu, 2006). Concentrated marine nutrient subsidies delivered by seabirds can influence island plant growth and species composition, food web structure, and ecosystem productivity (Polis and Hurd, 1996; Sanchez-Pinero and Polis, 2000; Croll et al., 2005; Vizzini et al., 2016). When nutrient subsidies are inhibited or interrupted, the consequences for ecosystem functioning can be far-reaching. For example, when changes in habitat availability or predation prevent nesting birds from providing marine nutrient subsidies, recipient terrestrial ecosystems become nutrient depleted and experience shifts in their ecosystem states (Maron et al., 2006; Fukami et al., 2006; Jones, 2010; Young et al., 2010). The extreme consequences of precluding nutrient subsidies has been demonstrated on islands of the Aleutian Archipelago, where fox predation of seabirds has caused these ecosystems to shift entirely from grassland to tundra (Croll et al., 2005).

While there is a substantial understanding of the role of seabirds in ocean-island nutrient flows, there has been considerably less investigation of nutrient subsidies from mainland ecosystems to islands.

* Corresponding author at: College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia.
E-mail address: christinabuelow@gmail.com (C.A. Buelow).

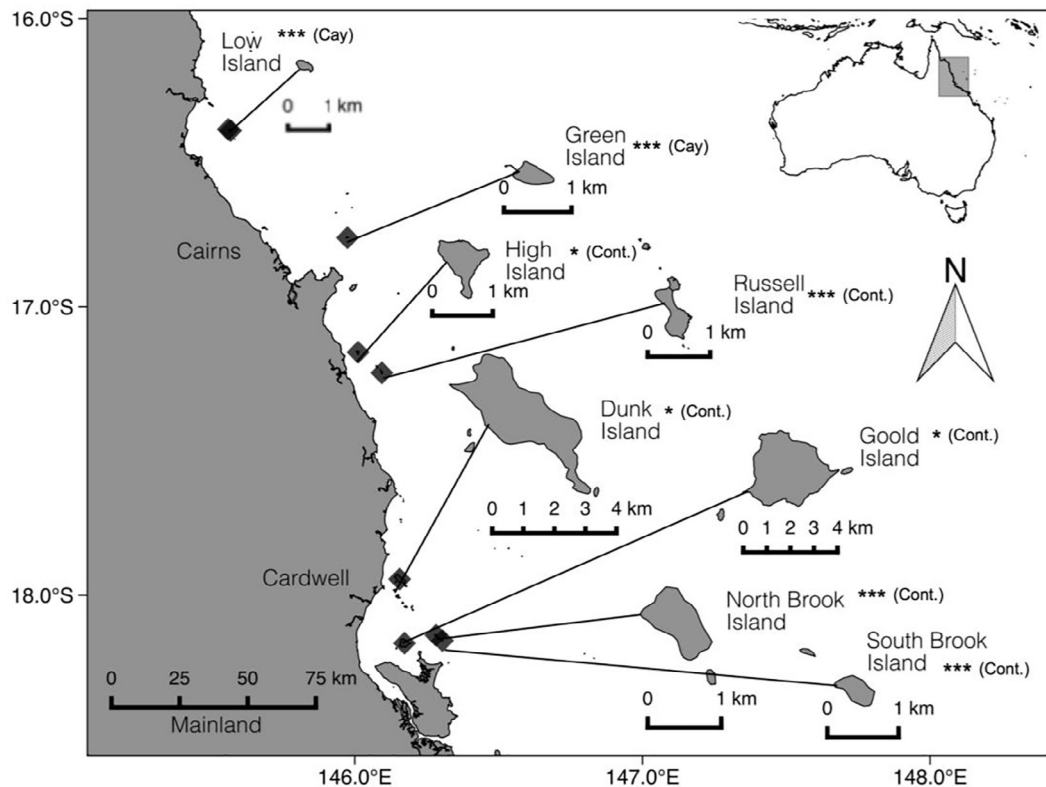


Fig. 1. Map of the eight study islands located along the northeast coast of Australia. Diamonds show island position relative to the mainland, and each island is enlarged to show individual size and shape. Asterisks indicate TIP colony presence (***) or absence (°) in island forest sampling areas. Islands also differed by their geomorphology: Cay vs. Continental (Cont.).

To our knowledge, the only mainland-island nutrient flow that has been quantified is nutrient transfer to an island mangrove forest by fruit bats that forage in mainland terrestrial forests (Reef et al., 2014). However, also in northeast Australia, Torresian Imperial-Pigeons (*Ducula spilorrhoa*¹) make daily fruit-foraging migrations to mainland rainforests from islands where they breed colonially, providing an opportunity to further explore mainland-island nutrient subsidies.

The northeast Australian Torresian Imperial-Pigeon (TIP) population undertakes annual migrations from southern Papua New Guinea to breed on islands along the northeast coast of Australia (Higgins and Davies, 1996). During the breeding season, TIPs make daily foraging migrations between island nesting habitat and mainland rainforest foraging habitat (Crome, 1975; Atherton and Greeves, 1985; Thorsborne et al., 1988; King, 1990; Brothers and Bone, 2012; Winter et al., 2016). The high degree of localized connectivity facilitated by the daily movements of TIPs is potentially an important process whereby large amounts of nutrients are exported from mainland coastal rainforests to nesting islands. The large size and range of the northeast Australian TIP population (1000 to > 10,000 breeding pairs in medium or large breeding colonies on islands along ~1300 km of coastline; King, 1990; Brothers and Bone, 2012) also means that the localized connectivity they provide may extend to a regional scale. Although the northeast Australian TIP population has rebounded following declines linked to hunting, clearing of mainland rainforest foraging habitat, and cyclones; the carrying capacity of the region may be permanently reduced since ~60% of lowland coastal rainforest was cleared prior to the 1980s (Winter et al., 1987; Thorsborne et al., 1988; King, 1990;

Winter et al., 2016). As coastal development continues, there is a need to understand the role of TIPs in connecting mainland coastal and island ecosystems.

When investigating nutrient subsidies, nitrogen and carbon isotopic signatures (δN^{15} and δC^{13}) can provide information regarding their origin (e.g. enriched δN^{15} indicates subsidization by a higher trophic level, such as birds; Wainright et al., 1998; Reef et al., 2014; Vizzini et al., 2016). Additionally, levels of total nitrogen (N) and phosphorus (P) in an ecosystem provide a measure of nutrient subsidy quantity, which is important for understanding controls on ecosystem productivity (Polis et al., 1997). However, the quality of nutrient subsidies is often over-looked and can have equally important effects on ecosystem processes (Sitters et al., 2015). Nutrient subsidy quality is determined through ecological stoichiometry (ES) by measurement of carbon, nitrogen, and phosphorus ratios in either detrital matter or in organisms (C:N:P; Sterner and Elser, 2002; Sitters et al., 2015). Quantifying these nutrient subsidy parameters can determine the importance of ecological connectivity provided by mobile link organisms, and encourage the development of holistic management strategies that are required to maintain linkages between mainland and island ecosystems (Lundberg and Moberg, 2003).

This study assessed the relationships between Torresian Imperial-Pigeon breeding colony presence and indicators of nutrient subsidization. Specifically, this research quantified several key indicators of nutrient subsidization in soil and leaf samples from island forests with and without TIP colonies: 1) nutrient origin, as indicated by δN^{15} and δC^{13} , 2) nutrient quantity, as indicated by total carbon (C), nitrogen (N), and phosphorus (P) levels, and 3) nutrient quality and limitation, as indicated by C:N:P ratios.

¹ The most recent taxonomic review of the genus *Ducula* has classified the northeast Australian population as the Torresian Imperial-Pigeon (*Ducula spilorrhoa*) (BirdLife Australia, 2017). Previously, this population was classified as a Torresian subspecies (*Ducula bicolor spilorrhoa*) of the Pied Imperial-Pigeon (*Ducula bicolor*) (BirdLife Australia, 2017).

2. Methods

2.1. Island forest study areas

Forest areas of eight northeast Australian islands were selected and categorized as: ‘TIP colony absent’ (three island forests) or ‘TIP colony present’ (five island forests; Fig. 1). Forest sampling areas on each island were chosen for their accessibility (i.e. the ability to access islands by boat and cross terrain to enter forests). From each access point, nest searches were conducted to confirm TIP colony presence or absence in forest sampling areas during the previous breeding season. In addition to TIP colony presence/absence, island forests differed by their geomorphology (continental or cay island type; Fig. 1). Due to limited accessibility, cay islands without TIP colonies were not able to be included in the study design. Sedimentary differences between these two island types could confound assessment of nutrient origin, quantity, and quality in soil and leaf samples. Therefore, island type has been included as an additional variable when analysing the results of the present study (see Section 2.4 below).

2.2. Soil and leaf collection

All island forests were sampled at the end of the TIP breeding season (post-breeding season, February–March 2016). Four locations were randomly selected from within each island forest sampling area, and the closest suitable trees (*Mystrica muelleri*) and soil areas to each location were sampled. Soil samples were collected with a soil core (diameter = 3 cm, depth = 5 cm; total = 4 samples/island forest) and five leaves from each tree were collected (total = 4 trees/island forest). *Mystrica muelleri* was chosen for leaf sampling due to its common presence in rainforests of northeast Queensland, Australia. Following collection, all soil and leaf samples were stored frozen until further analysis.

2.3. δN^{15} , δC^{13} , carbon, nitrogen, and phosphorus measurement

Soil samples were oven-dried at 60 °C to a constant dry weight (samples were weighed at 20 h and again at 24 h to ensure a constant dry weight had been achieved). Five leaves from each tree were pooled together, washed in distilled water, and then oven-dried at 60 °C to a constant dry weight (see protocol for soil). Leaves were pooled to encompass within-tree variability in leaf isotopic signatures and nutrient levels that may occur due to differences in light availability (Chapin et al., 1987).

Dried soil and leaf samples were homogenized with a bead mill and weighed into tin capsules. Subsequently, δN^{15} , δC^{13} , total carbon (C mg/g), and total nitrogen (N mg/g) were measured in parallel using a PDZ Europa ANCA-GSL elemental analyzer connected to a PDZ Europa 20–20 isotope ratio mass spectrometer at the University of California Davis Stable Isotope Facility, USA. All nitrogen and carbon stable isotope ratios were expressed in per mill (‰) using the δ notation:

$$\delta X = \left(\frac{R(\text{sample})}{R(\text{standard})} - 1 \right) \times 1000$$

where X refers to the element of interest (i.e. C or N) and R is the ratio of the heavier isotope to the lighter isotope of element X (i.e. $^{13}C/^{12}C$ or $^{15}N/^{14}N$). The δ values are presented relative to the international standard VPDB (Vienna PeeDee Belemnite) for $\delta^{13}C$, and Air for $\delta^{15}N$.

For total phosphorus levels (P mg/g), dried soil and leaf samples were analysed for total acid extractable P at the Environmental Analysis Laboratory (Southern Cross University, Australia). Samples were digested on a hotblock digester using an Aqua Regia solution (1:3) Nitric acid/Hydrochloric acid, and then read on an ICP-MS (EPA3050B and APHA 3125 ICPMS).

2.4. Data analysis

2.4.1. Forest classification

Principal components analysis (PCA) on a correlation matrix was used to visualise the relationships among variables measured in soil and leaf samples (i.e. δN^{15} , δC^{13} , and total N, P, and C) from island forests categorized as ‘TIP colony present’ or ‘TIP colony absent’.

2.4.2. Importance of nutrient subsidies

Random Forest is a non-parametric technique that is derived from classification and regression trees (CARTs), but uses an ensemble learning algorithm to build a ‘forest’ of un-pruned trees for improved predictive accuracy (Breiman, 2001; Cutler et al., 2007). Trees are grown using bootstrap samples of the original data, where a third is left out for validation (i.e. out-of-bag (OOB)) (Breiman, 2001; Cutler et al., 2007). The Gini index splitting rule (Breiman et al., 1984) finds the most homogeneous subgroups of the data given a randomised subset of the predictor variables, and the misclassification rate for OOB observations is aggregated across all trees in the ‘forest’ (Breiman, 2001; Cutler et al., 2007). The relative importance of each predictor variable to the predictive accuracy of the Random Forest is determined by randomly permuting OOB values, and then calculating the difference between OOB error estimates for actual vs. randomly permuted values and dividing by the standard error (Cutler et al., 2007). Finally, variable dependence plots can be used to visualise variable relationships by plotting the predicted response as a function of a predictor variable of interest (Friedman, 2000).

We used Random Forest models to determine the relative importance and relationship of individual variables measured in soil and leaf samples to the classification of island forests as ‘TIP colony present’ or ‘TIP colony absent’. In addition to nutrient subsidy indicators, island type (i.e. continental or cay) was included as a variable to determine its importance in forest classification. Random Forests of 1000 trees in size were grown using the Gini index splitting rule (Breiman et al., 1984), and out-of-bag (OOB) error estimates (i.e. the misclassification rate) were calculated to obtain a measure of model fit for each Random Forest. The importance of each variable to the predictive accuracy of soil and leaf Random Forest models was also calculated. High variable importance values indicate that the variable of interest increases the predictive accuracy of the Random Forest model, while values ≤ 0 indicate that the variable of interest either does not contribute, or detracts, from the predictive accuracy.

The relationship between individual nutrient subsidy variables and the probability of island forest classification as ‘TIP colony present’ was further investigated with variable dependence plots. Variable dependence plots show the probability of classifying island forests as ‘TIP colony present’ as a function of each variable measurement. Loess smoothers with 95% confidence intervals were overlaid on the variable dependence plots to aid in visualization of the relationship between nutrient subsidy variables and the probability of TIP colony presence.

All statistical analyses were performed in R version 3.3.2 (R Core Team, 2016). PCA plots were created with the package ‘ggbiplot’ (Vu, 2011), and Random Forest models were analysed and displayed with the packages ‘randomForestSRC’ and ‘ggRandomForests’, respectively (Ishwaran and Kogalur, 2017; Ehrlinger, 2016). Raw variable measurements (\pm standard error) have been included in the Supplementary materials (Appendix 1: isotopic signatures, Appendix 2: total C, N, and P; Appendix 3: C:N:P ratios).

3. Results

3.1. Forest classification

Principal components one (PC1) and two (PC2) for soil samples explained 78.2% of the variability in δN^{15} , δC^{13} , total C (mg/g), total N (mg/g), and total P (mg/g) among island forest areas sampled in the

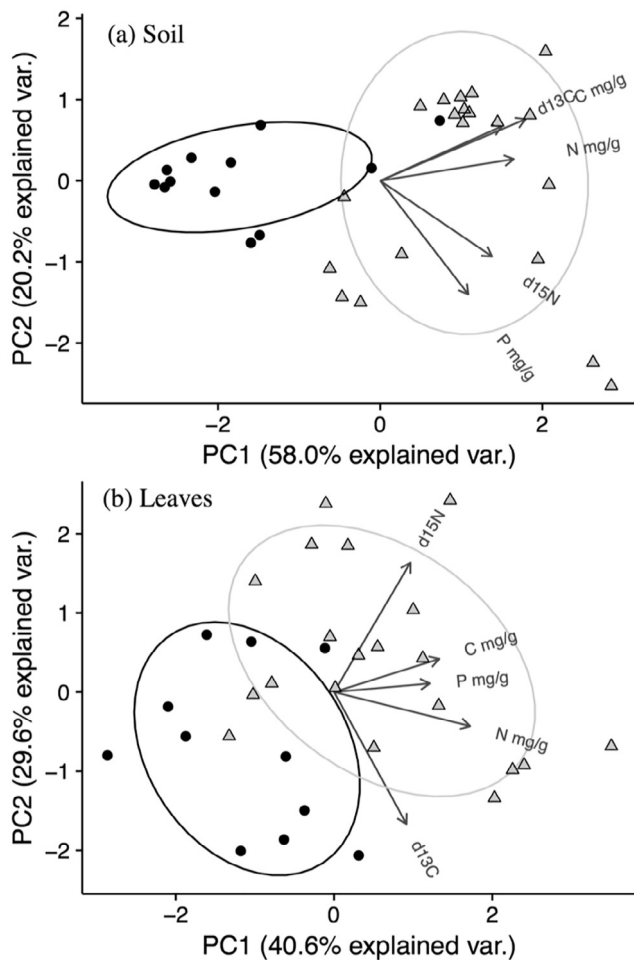


Fig. 2. Principal components analysis showing the relationship between island forests categorized as ‘TIP colony present’ (grey triangles) or ‘TIP colony absent’ (black circles) and the following soil (a) and leaf (b) nutrient subsidy indicators: δN^{15} (d15N), δC^{13} (d13C), total nitrogen (N mg/g), total phosphorus (P mg/g), and total carbon (C mg/g).

present study (Fig. 2 a). Soil total N and C, and δC^{13} variables were primarily correlated with PC1, with highest values in forest areas where TIP colonies were present (Fig. 2a). Soil total P and δN^{15} variables were not primarily correlated with either principal component, and their highest values were also in forest areas with TIP colonies present (Fig. 2a).

For leaf samples, principal components one (PC1) and two (PC2) explained 70.2% of the variability in δN^{15} , δC^{13} , total C (mg/g), total N (mg/g), and total P (mg/g) among island forest areas sampled in the present study (Fig. 2b). Leaf total C, N, and P variables were primarily correlated with PC1, with highest values in forest areas with TIP colonies present (Fig. 2b). Conversely, δN^{15} and δC^{13} were oppositely correlated along PC2, with the highest values of δN^{15} in forest areas with TIP colonies present (Fig. 2b).

3.2. Importance of nutrient subsidies

3.2.1. Model fit

The soil Random Forest model had an overall OOB error rate of 9.68%, while the leaf Random Forest model had an overall OOB error rate of 17.24%.

3.2.2. Variable importance

When soil nutrient subsidy measurements were used to classify island forests as ‘TIP colony present’ or ‘TIP colony absent’, all variables except for island type contributed to the predictive accuracy of the

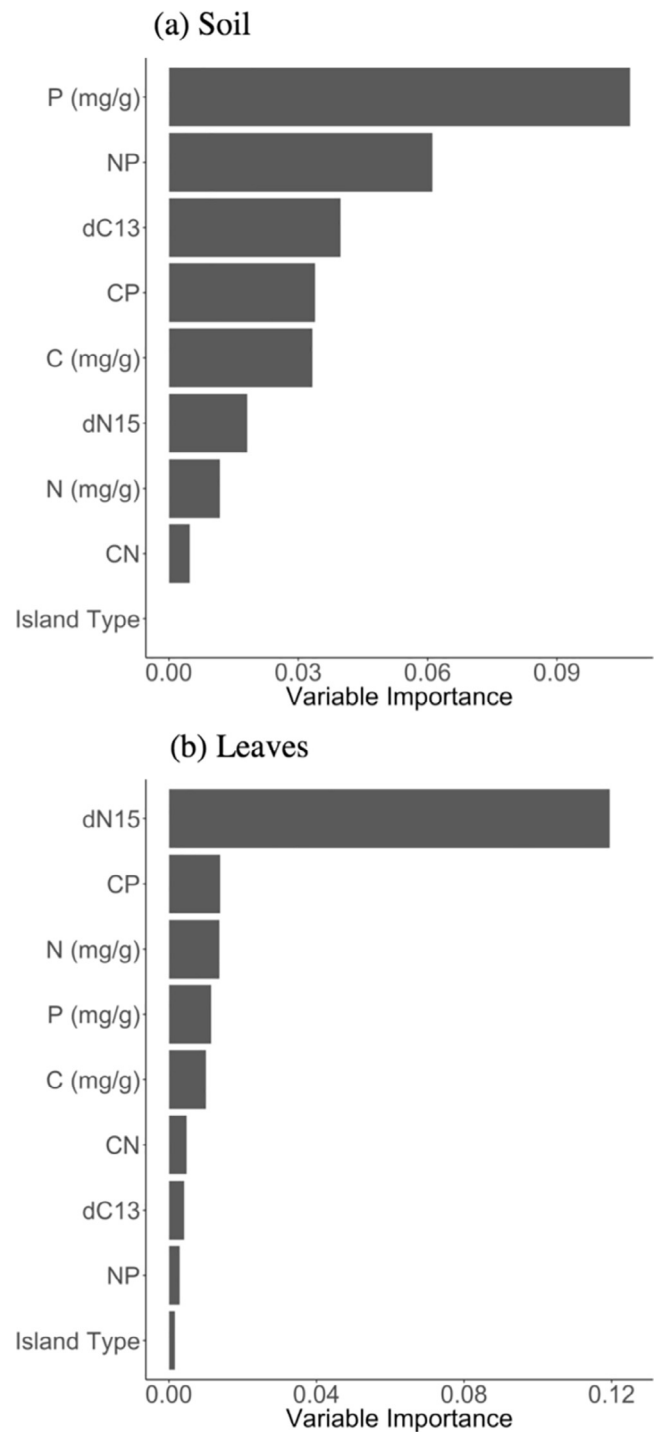


Fig. 3. Importance of variables measured in (a) soil and (b) leaf samples for classifying island forests as ‘TIP colony present’ or ‘TIP colony absent’. Variables with high importance values contribute to the predictive accuracy of the Random Forest model used for classification, while a value of zero indicates that the variable does not contribute to the predictive accuracy. (Note: dN15 = δN^{15} and dC13 = δC^{13} .)

Random Forest model (Fig. 3a). Total phosphorus, N:P, and δC^{13} were the three most important soil nutrient subsidy indicators in island forest classification (Fig. 3a). Alternatively, when leaf nutrient subsidy measurements were used to classify island forests as ‘TIP colony present’ or ‘TIP colony absent’, δN^{15} was the only substantially important variable (Fig. 3b). ‘Island type’ also had low variable importance in the leaf Random Forest model (Fig. 3b), and therefore ‘island type’ was not included in further analysis of variable dependence (see subsections

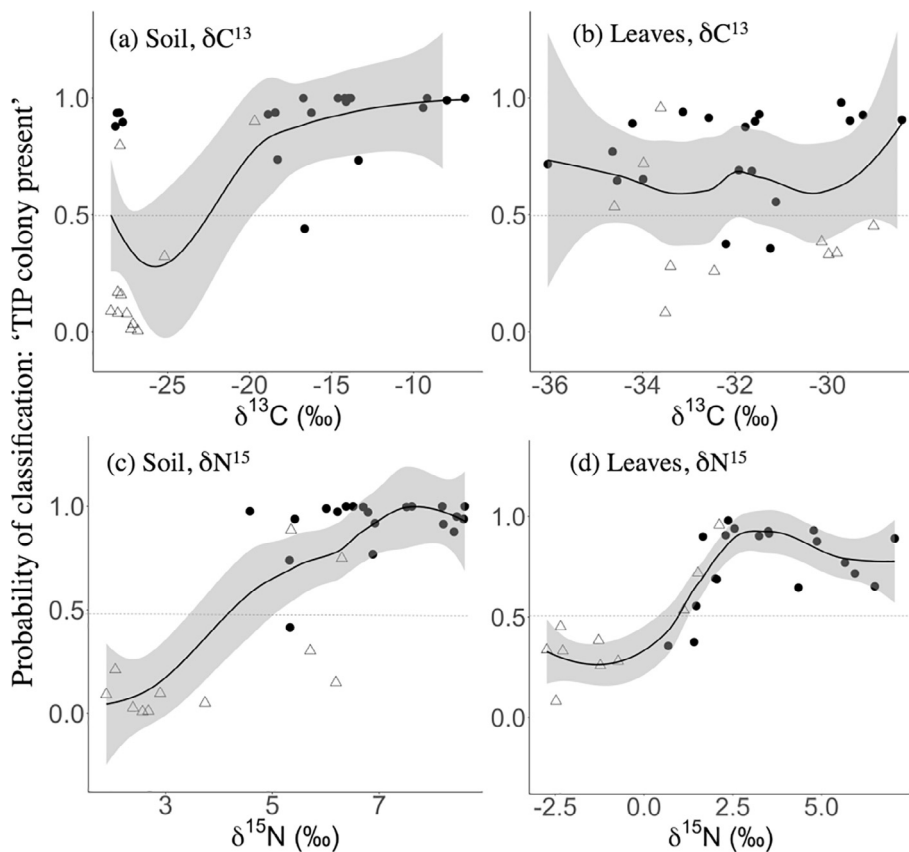


Fig. 4. Variable dependence plots for carbon (δC^{13}) and nitrogen (δN^{15}) stable isotope signatures in soil (a & c) and leaf (b & d) samples. A loess smoother (with a 95% confidence interval) shows the relationship between the isotopic signature (δC^{13} or δN^{15}) and probability of classification as 'TIP colony present' by the Random Forest model. Symbols represent the category to which individual measurements belong ('TIP colony absent' = white triangles, and 'TIP colony present' = black circles). The grey-dashed line indicates 50% probability of classification as 'TIP colony present'.

below).

3.2.3. Variable dependence: nutrient origin (δN^{15} and δC^{13})

Variable dependence plots show how individual variable measurements are related to the probability of island forests being classified as 'TIP colony present'. Soil δC^{13} values increased as the probability of TIP colony presence increased (Fig. 4a). In contrast, there was no clear relationship between leaf δC^{13} values and the probability of TIP colony presence (Fig. 4b). For δN^{15} , values in soil and leaves increased as the probability of classification as 'TIP colony present' increased (Fig. 4c, d).

3.2.4. Variable dependence: total nutrient levels (C, N, P) and ratios (C:N:P)

Total C, N, and P levels increased as the probability of classification as 'TIP colony present' increased for both soil and leaf samples (Fig. 5). In contrast, soil N:P and C:P nutrient ratios increased with decreasing probability of classification as 'TIP colony present' (Fig. 6a, e), and there was no clear relationship with soil C:N nutrient ratios (Fig. 6c). For leaves, there was also no clear relationship between N:P and probability of classification as 'TIP colony present' (Fig. 6b), while leaf C:N and C:P ratios decreased as the probability of classification as 'TIP colony present' increased (Fig. 6d, f).

4. Discussion

Torresian Imperial-Pigeons clearly provide a nutrient subsidy to island forests of northeast Australia where they breed colonially. The foraging behaviour of Australia's northeast TIP population has been well studied, to the extent that the standard method for estimating colony size is counting individuals as they return to their island nesting sites from foraging in mainland rainforests (Atherton and Greeves, 1985; Thorsborne et al., 1988; King, 1990; Brothers and Bone, 2012;

Winter et al., 2016). This suggests that a high proportion of the nutrients they deliver to islands will be rainforest-derived, supporting the growing body of literature acknowledging the importance of cross-ecosystem nutrient flows (Sitters et al., 2015) and building a case for classifying TIPs as a mobile-link species in facilitating these processes. However, it is possible that individuals may also forage in island forests with fruiting trees. Tracking studies would provide a better understanding of the localized foraging movements of TIPs and determine what proportion of the nutrients that they deliver to their island nesting grounds are derived from mainland rainforests.

4.1. Breeding colonies enrich δN^{15} and elevate nutrient levels

Nutrient subsidies are clear from δN^{15} enrichment and increased nitrogen and phosphorus levels in island forests where TIP colonies are likely to be breeding. Guano enriches soil and leaf δN^{15} through mechanisms including: microbial nutrient cycling, trophic enrichment, and ammonia volatilization (Natelthofer and Fry, 1988; Wainright et al., 1998). Also, the high concentrations of phosphorus and nitrogen in guano have made it extremely valuable as a mined resource (for use in fertilizer, explosives, etc.), causing wars over claims to seabird islands in the 1800's (Whelan et al., 2008, 2015). In the present study, total phosphorus was the most important soil nutrient subsidy indicator of TIP colony presence, while δN^{15} was the most important leaf nutrient subsidy indicator. The δN^{15} enrichment of leaves (~7‰) was not as high as terrestrial plants found near seabird colonies (e.g. ~22‰, Wainright et al., 1998), and this is likely the result of TIP's diet of fruit causing lower trophic enrichment. Similarly low levels of foliar δN^{15} enrichment have been found in the roosting areas of frugivorous bats (3–4‰, Reef et al., 2014).

The presence of TIP breeding colonies was also related to island forest δC^{13} enrichment, however the effect differed for soil and leaf samples. In soil samples both δC^{13} values and total carbon levels

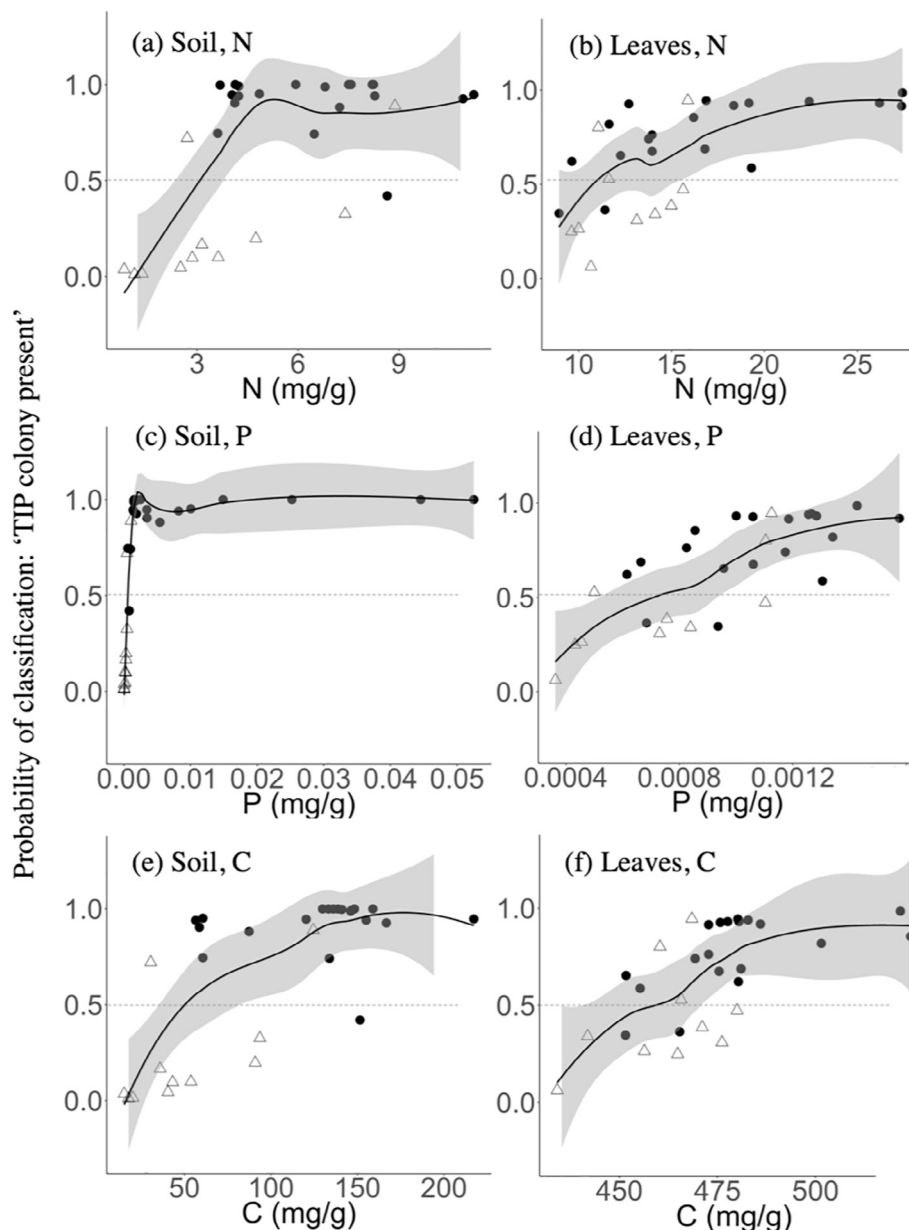


Fig. 5. Variable dependence plots for total nitrogen (mg/g), phosphorus (mg/g), and carbon (mg/g) in soil (a, c, e) and leaf (b, d, f) samples. A loess smoother (with a 95% confidence interval) shows the relationship between the variable measurement and probability of classification as 'TIP colony present' by the Random Forest model. Symbols represent the category to which individual measurements belong ('TIP colony absent' = white triangles, and 'TIP colony present' = black circles). The grey-dashed line indicates 50% probability of classification as 'TIP colony present'.

increased in island forests with high likelihood of TIP colony presence. High total carbon levels in soil samples were expected in response to TIP colony presence (Garcia et al., 2002; Ellis, 2005), and soil δC^{13} enrichment could be related to higher biomass of δC^{13} -enriched leaf litter below TIP colonies. However, there was no relationship between leaf δC^{13} values and the probability of TIP colony presence. This contrasts other studies that have found leaf δC^{13} enrichment in areas near bird colonies, likely due to higher leaf nitrogen levels and plant growth rates (Wainright et al., 1998; Cordell et al., 1999; Adame et al., 2015). It is possible that variation in leaf δC^{13} enrichment could be related to differential light availability for individual plants that were sampled in the present study (Buchmann et al., 1997), something worth controlling for in future studies.

Due to seasonality in the timing of breeding, nutrient deposition by colonial birds can be temporally variable and may result in a seasonal nutrient pulse to recipient ecosystems (Hahn et al., 2008; Adame et al.,

2015). Torresian Imperial-Pigeons breed on islands of Australia's northeast coast only during the summer months, and this may cause intra-annual variability in breeding island nutrient levels. However, further research on nutrient flows outside of the breeding season is needed to fully understand how nutrient pulses may influence the functioning of these island forest ecosystems.

4.2. Nutrient limitation and enhanced nutrient quality in response to TIP nutrient subsidies

Nitrogen and phosphorus are often limiting nutrients in terrestrial ecosystems (Tessier and Raynal, 2003; Gusewell, 2004; Vitousek et al., 2010). Nutrient limitation can be inferred from increased leaf nutrient uptake in response to increased availability in soil, and also by leaf N:P ratios (Vitousek et al., 2010). Soil nitrogen and phosphorus levels were elevated in island forests with high probability of TIP colony presence

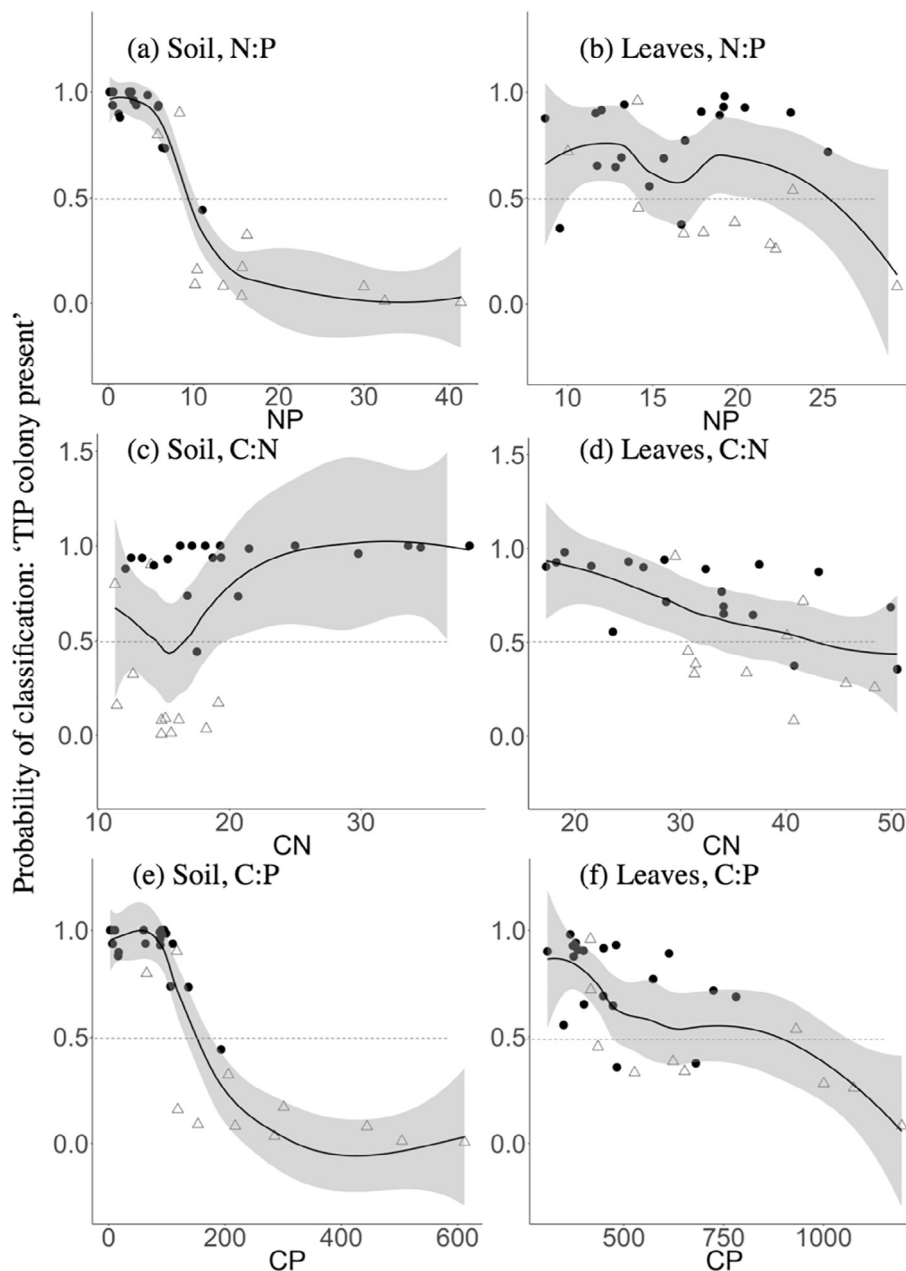


Fig. 6. Variable dependence plots for N:P, C:N, and C:P in soil (a, c, e) and leaf (b, d, f) samples. A loess smoother (with a 95% confidence interval) shows the relationship between the variable measurement and probability of classification as ‘TIP colony present’ by the Random Forest model. Symbols represent the category to which individual measurements belong (‘TIP colony absent’ = white triangles, and ‘TIP colony present’ = black circles). The grey-dashed line indicates 50% probability of classification as ‘TIP colony present’.

and, if plants were limited by either of these nutrients, leaf nutrient levels should show similar relationships (Tessier and Raynal, 2003). Indeed, leaf nitrogen and phosphorus levels increased as the probability of TIP colony presence increased, suggesting that island forests in the present study may be co-limited by both nitrogen and phosphorus.

Leaf N:P ratios provide additional support for nutrient co-limitation in island forests of the present study. Generally, low leaf N:P ratios mean that plants are nitrogen limited while high leaf N:P ratios demonstrate phosphorus limitation (Tessier and Raynal, 2003). However, leaf N:P ratios did not show a clear increase or decrease with probability of TIP colony presence, suggesting either a lack of limitation or, alternatively, co-limitation by both nutrients. When nitrogen or phosphorus are not limiting, other factors can influence leaf N:P ratios such as: light, soil water, and temperature (Aerts and Chapin, 2000; Tessier and Raynal, 2003). Further research that includes measurement of potential confounding variables and larger sample size would improve

our understanding of leaf N:P ratios and nutrient limitation. Although soil N:P ratios are not indicative of plant nutrient limitation, soil N:P decreased with increasing probability of TIP colony presence. This relationship is similar to low soil N:P ratios that were measured on islands subsidized by cormorant breeding colonies (Kolb et al., 2013).

Nutrient subsidization by TIP breeding colonies appears to enhance island forest nutrient quality and plant growth. Nutrient quality is directly related to plant growth rate, and can be inferred from C:nutrient ratios. The growth rate hypothesis states that low leaf C:N and C:P ratios are diagnostic of high plant nutrient quality and growth rate (Agren, 2004, 2008; Rong et al., 2015). Additionally, low soil C:N and C:P ratios have been measured in areas that receive nutrient subsidization by seabirds (Maron et al., 2006; Jones, 2010; Kolb et al., 2013). In the present study, soil C:P ratios decreased as probability of TIP colony presence increased; however, soil C:N ratios did not show a definitive trend. Additionally, leaf C:N and C:P ratios decreased as the

probability of TIP colony presence increased. Overall, these relationships suggest that nutrient quality and plant growth rates increase in island forests where TIP breeding colonies are likely to occur.

Although enhanced plant growth in response to Torresian Imperial-Pigeon breeding colony presence is likely, plant growth rate should be measured directly in future studies. More research is also needed to better understand why enriched soil δC^{13} values were associated with TIP colony presence. Finally, because this was not a comprehensive study of all effects of TIP nutrient transfer for island ecosystem functioning, the consequences of island nutrient subsidies can extend beyond those examined here. For example, seabird nutrient subsidies can increase the abundance of island invertebrates, such as soil nematodes (Townes et al., 2009). Concentrated bird nutrient subsidies can also leach from islands to adjacent marine ecosystems, elevating nitrogen and phosphorus levels in algae, or increasing seagrass biomass (Powell et al., 1991; Kolb et al., 2010, 2013). This merely hints at the great multitude of possibilities for further investigation of TIP nutrient flows, such as primary/secondary production and species composition in recipient island forests, and nutrient leaching to adjacent marine areas.

4.3. Implications

Given their role as a nutrient subsidy vector, Torresian Imperial-Pigeons should be classified as an avian mobile-link species that is necessary for the functioning and resilience of island ecosystems. Maintaining TIP nutrient flows will require effective conservation of their mainland foraging habitat and island forest nesting habitat. A successful strategy will also require consideration of the northeast Australian TIP population's migratory breeding behaviour. The abundance of fruit in coastal lowland rainforests of northeast Australia, and the availability of nearby islands that may offer protection from nest-predation and anthropogenic disturbance, likely create ideal conditions for TIPs to form dense breeding colonies and make daily foraging migrations (King, 1990; Hazel and Venables, 2017). Therefore, the availability and connectivity of mainland and island habitats is likely to be necessary for sustaining the annual migration of TIPs from southern Papua New Guinea.

Currently, some of the breeding island forests sampled in the present study are protected as National Parks (e.g. North Brook Island and Green Island; Queensland Government, 2017). However, TIPs undertake both daily localized foraging migrations and annual long-distance migrations, suggesting that a broader strategy that integrates across local, regional, and inter-continental spatial scales is warranted (Stoms et al., 2005). Similar arguments have been made when investigating the importance of stopover sites for shorebirds during their long-distance migrations. Connectivity between roosting and foraging areas within stopover sites is needed for shorebirds to acquire enough energy for the broader success of their long-distance migration (Farmer and Parent, 1997; Dias et al., 2006; Oberneufemann et al., 2013). Therefore, although long-distance movements are perhaps more obvious, there is a need to understand the localized movements of migrants, and the drivers and consequences of the connectivity they may require or facilitate.

Acknowledgements

We gratefully acknowledge Dr Carlo Mattone and Jakob Fries for assistance in accessing field sites, and to the following for their funding support: Wet Tropics Management Authority, Birds Queensland, BirdLife Australia, and Ecological Society of Australia. This research was conducted in accordance with the Department of Environmental and Heritage Protection, Queensland (permit WITK16562315), and the Great Barrier Reef Coast Marine Park (permit QFN15/003).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2018.02.029>.

References

- Adame, M.F., Fry, B., Gamboa, J.N., Herrera-Silveira, J.A., 2015. Nutrient subsidies delivered by seabirds to mangrove islands. *Mar. Ecol. Prog. Ser.* 525, 15–24.
- Aerts, R., Chapin III, F.S., 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30, 1–67.
- Agren, G.I., 2004. The C:N:P stoichiometry of autotrophs – theory and observations. *Ecol. Lett.* 7, 185–191.
- Agren, G.I., 2008. Stoichiometry and nutrition of plant growth in natural communities. *Annu. Rev. Ecol. Syst.* 39, 153–170.
- Atherton, R.G., Greeves, D., 1985. Torresian imperial-pigeon *Ducula spilorrhoa* on Green Island, north-eastern Queensland. *Emu* 85, 261–263.
- BirdLife Australia, 2017. The BirdLife Australia Working List of Australian Birds; Version 2.1 Downloaded from http://www.birdlife.org.au/documents/BWL-BirdLife_Australia_Working_List_v2.1.xlsx.
- Breiman, L., Friedman, H., Olshen, A., Stone, C.J., 1984. Classification and Regression Trees. Wadsworth and Brooks/Cole, Monterey, California, USA.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 15–32.
- Brothers, N., Bone, C., 2012. Torresian Imperial Pigeon *Ducula spilorrhoa* monitoring, population trends and species suitability as an indicator of environmental change. *Corella* 36, 69–75.
- Buchmann, N., Kao, W., Ehleringer, J., 1997. Influence of stand structure on carbon-13 of vegetation, soil, and canopy air within deciduous and evergreen forests in Utah, United States. *Oecologia* 110, 109–119.
- Chapin, F.S., Bloom, A.J., Field, C.B., Waring, R.H., 1987. Plant responses to multiple environmental factors. *Bioscience* 37, 49–57.
- Cordell, S., Goldstein, G., Meinzer, F.C., Handley, L.L., 1999. Allocation of nitrogen and carbon in leaves of *Metrosideros polymorpha* regulates carboxylation capacity and δC^{13} along an altitudinal gradient. *Funct. Ecol.* 13, 811–818.
- Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M., Byrd, G.V., 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* 307, 1959–1961.
- Crome, F.H.J., 1975. Breeding, feeding and status of the Torres Strait pigeon at Low Isles, north-eastern Queensland. *Emu* 75, 189–198.
- Cutler, R.D., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. *Ecology* 88, 2783–2792.
- Dias, M.P., Granadeiro, J.P., Lecoq, M., Santos, C.D., Palmeirim, J., 2006. Distance to high-tide roosts constrains the use of foraging areas by dunlins: implications for the management of estuarine wetlands. *Biol. Conserv.* 13, 446–452.
- Ehrlinger, J., 2016. ggRandomForests: Visually Exploring Random Forests. R Package Version 2.0.1.
- Ellis, J.C., 2005. Marine birds on land: a review of plant biomass, species richness and community composition in seabird colonies. *Plant Ecol.* 181, 227–241.
- Farmer, A.H., Parent, A.H., 1997. Effects of landscape on shorebird movements at spring migration stopovers. *The Condor* 99, 698–707.
- Friedman, J.H., 2000. Greedy function approximation: a gradient boosting machine. *Ann. Stat.* 29, 1189–1232.
- Fukami, T., Wardle, D.A., Bellingham, P.J., Mulder, C.P.H., Towns, D.R., Yeates, G.W., Bonner, K.I., Durrett, M.S., Grant-Hoffman, M.N., Williamson, W.M., 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecol. Lett.* 9, 1299–1307.
- Garcia, L.V., Maranon, T., Ojeda, F., Clemente, L., Redondo, R., 2002. Seagull influence on soil properties, chenopod shrub distribution and leaf nutrient status in semi-arid Mediterranean islands. *Oikos* 98, 75–86.
- Gunderson, L.H., 2000. Ecological resilience – in theory and application. *Annu. Rev. Ecol. Syst.* 31, 425–439.
- Gusewell, S., 2004. N:P ratios in terrestrial plants: variation and functional significance. *New Phytol.* 164, 243–266.
- Hahn, S., Bauer, S., Klaassen, M., 2008. Quantification of allochthonous nutrient input into freshwater bodies by herbivorous waterbirds. *Freshwater Biol.* 53, 181–193.
- Hazel, J., Venables, B.L., 2017. Can island specialists succeed as urban pioneers? Pied imperial-pigeons provide a case study. *Wildl. Res.* 44, 40–47.
- Higgins, P.J., Davies, S.J.J.F. (Eds.), 1996. Handbook of Australia and New Zealand and Antarctic Birds. Vol. 3: Snipe to Pigeons. Oxford University Press, Melbourne.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Ishwaran, H., Kogalur, U.B., 2017. Random Forests for Survival, Regression and Classification (RF-SRC), R Package Version 2.4.2.
- Jones, H.P., 2010. Seabird islands take mere decades to recover following rat eradication. *Ecol. Appl.* 20, 2075–2080.
- King, B.R., 1990. Distribution and status of the Torresian Imperial Pigeon *Ducula spilorrhoa* in North-eastern Queensland: Cooktown to Cape York. *Emu* 90, 248–253.
- Kolb, G.S., Jerling, L., Hamback, P.A., 2010. The impact of cormorants on plant-arthropod food webs on their nesting islands. *Ecosystems* 13, 353–366.
- Kolb, G.S., Palmborg, C., Hamback, P.A., 2013. Ecological stoichiometry and density responses of plant-arthropod communities of on cormorant nesting islands. *PLoS One* 8, e61772. <http://dx.doi.org/10.1371/journal.pone.0061772>.
- Lundberg, J., Moberg, F., 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6, 87–98.
- Maron, J.L., Estes, J.A., Croll, D.A., Danner, E.M., Elmendorf, S.C., Buckelew, S.L., 2006.

- An introduced predator alters Aleutian island plant communities by thwarting nutrient subsidies. *Ecol. Monogr.* 76, 3–24.
- Natelhoffer, K.J., Fry, B., 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Sci. Soc. Am. J.* 52, 1633–1640.
- Oberneufemann, K.P., Collazo, J.A., Lyons, J.E., 2013. Local movements and wetland connectivity at a migratory stopover of semipalmated sandpipers (*Calidris pusilla*) in the southeastern United States. *Waterbirds* 36, 63–76.
- Polis, G.A., Hurd, S.D., 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am. Nat.* 147, 396–423.
- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28, 289–316.
- Powell, G.V.N., Fourqurean, J.W., Kenworthy, W.J., Zieman, J.C., 1991. Bird colonies cause seagrass enrichment in a subtropical estuary: observational and experimental evidence. *Estuar. Coast. Shelf Sci.* 32, 567–579.
- Queensland Government Department of National Parks, Sport and Racing (accessed April 11, 2017). <https://www.npsr.qld.gov.au/2017>.
- R Core Team, 2016. *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reef, R., Feller, I.C., Lovelock, C.E., 2014. Mammalian herbivores in Australia transport nutrients from terrestrial to marine ecosystems via mangroves. *J. Trop. Ecol.* 30, 179–188.
- Rong, Q., Liu, J., Cai, Y., Lu, A., Zhao, Z., Yue, W., Xia, J., 2015. Leaf carbon, nitrogen and phosphorus stoichiometry of *Tamarix chinensis* Lour in the Laizhou Bay coastal wetland, China. *Ecol. Eng.* 76, 57–65.
- Sanchez-Pinero, F., Polis, G.A., 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* 81, 3117–3132.
- Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. *Trends Ecol. Evol.* 21, 464–471.
- Sitters, J., Atkinson, C.L., Guelzow, N., Kelly, P., Sullivan, L.L., 2015. Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos* 124, 920–930.
- Sterner, R.W., Elser, J.J., 2002. *Ecological Stoichiometry: the Biology of Elements From Molecules to the Biosphere*. Princeton University Press.
- Stoms, D.M., Dais, F.W., Andelman, S.J., Carr, M.H., Gaines, S.D., Halpern, B.S., Hoenicke, R., Leibowitz, S.G., Leydecker, A., Madin, E.M.P., Tallis, H., Warner, R.R., 2005. Integrated coastal reserve planning: making the land-sea connection. *Front. Ecol. Environ.* 3, 429–436.
- Tessier, J.T., Raynal, D.J., 2003. Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. *J. Appl. Ecol.* 40, 523–534.
- Thorsborne, A.S., Thorsborne, M.G., Winter, J.W., 1988. Population changes of the Torresian Imperial-Pigeon *Ducula spilorrhoa* over twenty-one years on North Brook Island, North Queensland. *Emu* 88, 1–8.
- Towns, D.R., Wardle, D.A., Mulder, C.P.H., Yeates, G.W., Fitzgerald, B.M., Parrish, G.R., Bellingham, P.J., Bonner, K.I., 2009. Predation of seabirds by invasive rats: multiple indirect consequences for invertebrate communities. *Oikos* 118, 420–430.
- Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecol. Appl.* 20, 5–15.
- Vizzini, S., Signa, G., Mazzola, A., 2016. Guano-derived nutrient subsidies drive food web structure in coastal ponds. *PLoS One* 11, e0151018. <http://dx.doi.org/10.1371/journal.pone.0151018>.
- Vu, V., 2011. ggbiplot: A ggplot2 Based Biplot. R Package Version 0.55.
- Wainright, S.C., Haney, J.C., Kerr, C., Golovkin, A.N., Flint, M.V., 1998. Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. *Mar. Biol.* 131, 63–71.
- Whelan, C.J., Wenny, D.G., Marquis, R.J., 2008. Ecosystem services provided by birds. *Ann. NY. Acad. Sci.* 1134, 25–60.
- Whelan, C.J., Sekercioglu, C.H., Wenny, D.G., 2015. Why birds matter: from economic ornithology to ecosystem services. *J. Ornithol.* <http://dx.doi.org/10.1007/s10336-015-1229-y>.
- Winter, J.W., Bell, F.C., Pahl, L.I., Atherton, R.G., 1987. Rainforest clearfelling in northeastern Australia. *Proc. R. Soc. Queensland* 98, 41–57.
- Winter, J.W., Green, D., Thorsborne, M., Parsons, M., 2016. Population trends over 50 years of a Torresian Imperial-Pigeon breeding colony on North Brook Island, a tropical Great Barrier Reef island, Australia. *Emu* 116, 14–21.
- Young, H.S., McCauley, D.J., Dunbar, R.B., Dirzo, R., 2010. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *PNAS* 107, 2072–2077.