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

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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.

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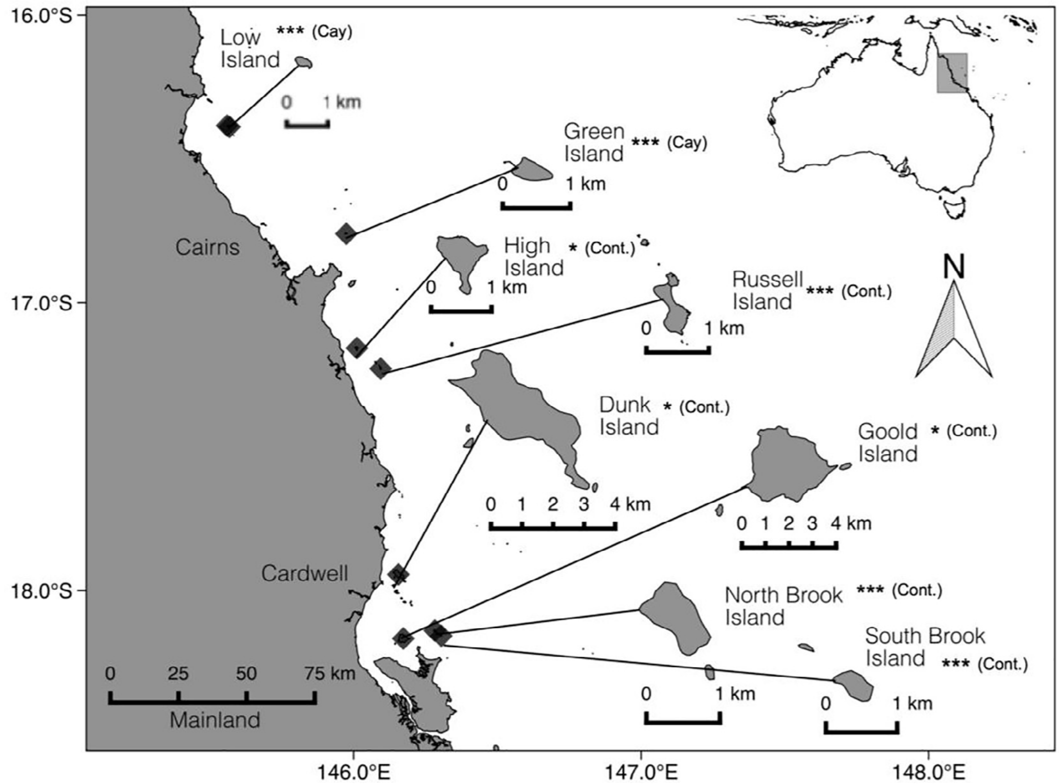

Fig. 1. Map of the eight study islands located along the northeast coast of Australia. Diamonds show island position relative to the mainland, and each island is enlarged to show individual size and shape. Asterisks indicate TIP colony presence (***) or absence (*) in island forest sampling areas. Islands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