From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems

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Human impact on biodiversity usually is measured by reduction in species abundance or richness. Just as important, but much more difficult to discern, is the anthropogenic elimination of ecological interactions. Here we report on the persistence of a long ecological interaction chain linking diverse food webs and habitats in the near-pristine portions of a remote Pacific atoll. Using biogeochemical assays, animal tracking, and field surveys we show that seabirds roosting on native trees fertilize soils, increasing coastal nutrients and the abundance of plankton, thus attracting manta rays to native forest coastlines. Partnered observations conducted in regions of this atoll where native trees have been replaced by human propagated palms reveal that this complex interaction chain linking trees to mantas readily breaks down. Taken together these findings provide a compelling example of how anthropogenic disturbance may be contributing to widespread reductions in ecological interaction chain length, thereby isolating and simplifying ecosystems.

From sea to land, from land to sea; And heave round earth, a living chain of interwoven agency. Goethe’s Faust

The chains of interactions that weave together the constituents of ecosystems are critical to their functioning. Such interaction chains include both trophic (e.g. consumption of prey by predators), informational (e.g. behavioral interactions), and abiotic (e.g. physical transport of nutrients across ecosystem boundaries) linkages that assemble both vertically (e.g. from top to bottom of food webs) and horizontally (e.g. across the boundaries of multiple food webs and habitats).

Alteration or elimination of any of the links in an ecological interaction chain can have deleterious and destabilizing effects on community and ecosystem functioning2–5. Some of these effects are direct, while others reach indirectly across ecosystems (e.g. change at one node in a chain influences another node via intermediary transmitter nodes6–7). There are many means by which human disturbance can negatively impact the integrity of ecological interaction chains. Species removals, species introductions, habitat conversions, pollution, and climate change can all change or abolish species interactions8–11. Given the sensitivity of these ecological links to anthropogenic change, we hypothesized that ecosystems more insulated from human influence may retain longer chains of ecological interactions that host linkages that bind these ecosystems closer together.

We conducted a focused empirical examination of this hypothesis by investigating the effects of anthropogenic disturbance on ecological interaction chain length at Palmyra Atoll, an especially remote collection of coral islets in the tropical central Pacific. The ecosystems of Palmyra have been much less impacted anthropogenically than many inhabited or heavily used coastal and island regions, but are by no means completely “pristine”12. Palmyra’s forests in particular have been altered by intermittent human activities. Historically large and contiguous patches of native forest, comprised principally of the native trees Pisonia grandis and Tournefortia argentea, have been threatened by the human-facilitated expansion of the coconut palm (Cocos nucifera)13,14. This type of anthropogenic disturbance is especially common in the tropics where palms of various species are aggressively cultivated for oil production at the expense of native forests15,16. Today, Palmyra’s forests are fractured into discrete patches of well conserved native forest surrounded by dense stands of coconut palm17 (Supplementary Fig. S1 and S2 online). This mosaic of recently disturbed habitats intermingled with generally more intact habitats provides a rare opportunity to test (by contrasting patterns in native and palm forests, Figure 1A) if and how human disturbance impacts interaction chain length.
Results

We initiated this comparison by examining how seabird utilization of forest canopies (e.g. as nesting and roosting habitat) differs in patches classified as either native or palm forest. Surveys of seabirds indicate that they show a strong preference for the complex and stable canopies of native forests, and a strong aversion for the simple and mobile canopies of palm forests. Resultant densities of seabirds in native forests are 4.8 times higher than palm forests (Figure 1B, Table 1). These divergent patterns of bird use have important effects on forest biogeochemistry. Soils in native forests are significantly elevated in plant available nitrogen—the likely limiting nutrient in this ecosystem (5.1 times higher than palm forests; Figure 1C, Table 1). It has been previously established that these changes in soil properties were caused by the importation and concentration of oceanic-derived nutrients in preferred nesting/roosting areas (e.g. guano) by these wide-ranging birds and that these changes do not pre-date forest alteration. Plants resident in native forests capitalize on these elevated nutrient levels, as is reflected by increased levels of foliar nitrogen in these sites (Figure 1D).

The influence of birds on forests extends beyond the boundaries of the terrestrial ecosystem. Water running off nutrient rich native forest islets into the marine environment carries with it 26.5 times higher loads of nitrogenous compounds than runoff from palm forests (Figure 1E). Data from moored, in-situ, phytoplankton growth chambers showed that relative changes in chlorophyll a (Chl a) were significantly higher in growth chambers situated along native forest coastlines, suggesting that nutrient additions in these zones may stimulate phytoplankton productivity (Table 1). In these same waters adjacent to native forests zooplankton are greater in biomass (Figure 1F) and certain zooplankton taxa (Copepoda) are larger (Table 1). Differences in the foraging ecology and behavior of a large and conspicuous obligate plankton consumer, the giant manta ray (Manta birostris), were also detected in native forest regions. In extensive visual surveys of mantas we documented that they are significantly more abundant along native forest coastlines than along palm forest coasts with similar bathymetry and morphology (Figure 1G; Supplementary Fig. S3 online). As a supplement to these visual surveys of mantas, we electronically tagged three adult individuals and tracked their movements. Tracking data showed the same pattern as visual surveys: mantas can and do range across the entire lagoon basin—but when they elect to use coastlines, tagged animals exclusively selected areas near native forests. We observed 86.4%, 78.4%, and 43.9% overlap of individual manta core use areas with native forest coastline. No overlap was observed by any of these animals with palm forest coastline.

The elevated nitrogen (N) isotope levels of seabird-derived nutrients (which result from the high trophic position of these predators) provide a convenient means for examining whether this complex string of ecological connections are causally connected to one another. Consistent with the hypothesis that manta rays are interactively linked to native forests via changes triggered by alterations in forest and seabird communities, we measured significantly higher δ¹⁵N levels indicative of utilization of seabird derived nutrients) at five key nodes in this long-range interaction chain (Figure 1; Table 2). The strength of this seabird isotope signal attenuates with increasing distance from the origin of this interaction chain (forests),
dynamics. The detectable presence of seabird-derived persistence along these native forest coasts represents an important abundant and active along these plankton rich native forest coasts. was that manta rays, which feed exclusively on plankton, were more observation that we made in these native forest associated habitats forest-facilitated, seabird-vectored nutrient additions. The last key observed patterns in the plankton is that they are responding to the productive, zooplankton are more abundant, and key zooplankton forest areas. Many of the nutrients concentrated in these native forests defining biogeochemical patterns of both plants and soils in native birds. These seabirds vector large quantities of marine-derived mate- for seabirds and thus help to maintain high local abundances of sea- mechanisms. Native trees provide needed nesting/roosting habitat diverse series of trophic, non-trophic (behavioral), and physical processes in these forests to the ecology of manta rays through a Ecological interaction chains in the native forests of Palmyra connect Discussion

Ecological interaction chains in the native forests of Palmyra connect processes in these forests to the ecology of manta rays through a diverse series of trophic, non-trophic (behavioral), and physical mechanisms. Native trees provide needed nesting/roosting habitat for seabirds and thus help to maintain high local abundances of seabirds. These seabirds vector large quantities of marine-derived materials into the nutrient impoverished atoll terrestrial communities defining biogeochemical patterns of both plants and soils in native forest areas. Many of the nutrients concentrated in these native forests are returned to the adjacent oligotrophic ocean waters via rain and tidal vectoring. Sampling of the plankton communities directly along these native forest coastlines revealed that phytoplankton are more productive, zooplankton are more abundant, and key zooplankton taxa achieve larger sizes. The most parsimonious explanation for these observed patterns in the plankton is that they are responding to the forest-facilitated, seabird-vectored nutrient additions. The last key observation that we made in these native forest associated habitats was that manta rays, which feed exclusively on plankton, were more abundant and active along these plankton rich native forest coasts. While manta rays are wide ranging animals, this attraction to and persistence along these native forest coasts represents an important and unexpected link between their foraging ecology and forest dynamics. The detectable presence of seabird-derived δ15N materials in terrestrial, intertidal, subtidal, and pelagic organisms situated along this interaction pathway provides compelling support that this is indeed a unified long chain of dependant interactions. Sampling of other potential N sources in this system has revealed no evidence of alternative allochthonous or autochthonous origin materials which could have otherwise created these δ15N patterns.

This series of connections defines one of the longest ecological interaction chains yet observed in nature20–23. Other work has demonstrated that the majority of species involved in ecological interactions are only two links apart24. The interaction chain linking trees to manta rays in Palmyra’s native forests is at least five linkages long. The circuitous architecture of this particular interaction chain is as noteworthy as its length. This interaction presents an interesting route through which oceans affect change on land, and changes on land can feed back to influence ecological processes in the oceans (Figure 1). Reports of unidirectional transboundary ecological connections have garnered much attention25–27 – but this example of a complex bi-directional interaction adds to our understanding of the degree to which ecosystems can be interconnected. This interaction includes an interesting mix of both top-down (i.e. loss of birds affects plant and soil ecology) and bottom-up ecological effects (i.e. increases in bird-derived nutrients appears to increase plankton abundance). Instances of complex top-down and bottom-up interactions may be quite common in nature, but good empirical examples of these dynamics are as yet still emerging27.

We posit that this long interaction chain present in and near the native forests of Palmyra is maintained by the relative lack of human disturbance in the better protected parts of this unusually remote site. Data collected from our altered palm sites support this conclusion by demonstrating that forest alteration severely degrades the efficacy of this series of interactions (Figure 1). The corruption of these interactions very likely has a major negative affect upon the strength of the cross-taxonomic and cross-system connections that they supported. Observations from other systems suggest that many complex ecological interaction chains and associated sources of connectivity may be similarly vulnerable to anthropogenic perturbation. The introduction of non-native predators to Aleutian Islands caused

### Table 1 | Comparisons of processes in less disturbed native forests to those in more altered palm forests. Paired comparisons (pooled and analyzed by date) were made for all responses that were sampled repeatedly over time *. Np represents the total number of measurements conducted. Np (unpaired comparisons only) represents the number of replicates included in all statistical analyses after measurements were pooled at the level of transect for analysis. Np (paired comparisons only) represents the number of temporal comparisons included in analyses where repeated sampling was conducted over time. Parametric or nonparametric test statistics are reported for each comparison. Data collection was distributed equally between native and palm forests.

| Response                          | Native forests | Palm forests | t or W | P   | Np | Np | Np |
|----------------------------------|----------------|--------------|--------|-----|----|----|----|
| % cover native trees             | 83.6 (± 2.0)   | 20.5 (± 9.6) | 10.6 (8)| <0.0001 | 10 | 10 | - |
| Bird biomass (g m⁻² coastline)   | 515.7 (± 60.2)| 107.1 (± 22.8)| 9.5 (8)| <0.0001 | 46 | 10 | - |
| Soil nitrogen (NO₃⁻ + NH₄⁺; µg/g) | 201.5 (± 63.0)| 39.7 (± 10.5)| 3.6 (23)| <0.001 | 25 | 25 | - |
| % foliar nitrogen                | 3.7 (± 0.2)    | 2.5 (± 0.4)  | 3.0 (12)| 0.01  | 14 | 14 | - |
| Runoff water nitrogen (NO₃⁻; ppm) * | 0.18 (± 0.1)  | 0.01 (± 0.001)| 4.1 (7)| <0.01 | 51 | 8  | - |
| % change in Chl a *              | 372.5 (± 96.3) | 291.9 (± 102.1)| 5.0 (4)| <0.01 | 47 | -  | 5  |
| Zooplankton biomass (g m⁻³) *    | 0.13 (± 0.04)  | 0.04 (± 0.01)| 4.0 (7)| <0.01 | 77 | -  | 8  |
| Copepod length (mm) *           | 1.03 (± 0.03)  | 0.97 (± 0.03)| 2.2 (8)| 0.06  | 4,970 | 9  | - |
| No. individual mantas (survey min⁻¹) *† | 0.07 (± 0.02)  | 0 (± 0)      | 105 | <0.01 | 196 | -  | 21 |

### Table 2 | Comparisons of the δ15N of materials associated with native and palm forests. Differences in zooplankton δ15N were evaluated using paired comparisons (pooled by date; indicated with *) owing to their rapid turnover. All other parameters were compared using unpaired tests. Np represents the total number of measurements conducted. Np (zooplankton only) denotes the number of temporal comparisons conducted. Sampling was evenly split between native and palm forest sites.

| Response            | Native forests | Palm forests | t (df) | P   | Np | Np |
|---------------------|----------------|--------------|--------|-----|----|----|
| Soils               | 16.6 (± 0.9)   | 10.4 (± 1.1) | 4.4 (16)| <0.001| 18 | - |
| Tree leaves (T. argentea) | 15.4 (± 1.3) | 8.3 (± 2.3) | 2.6 (12)| 0.01| 14 | - |
| Intertidal clams (Macoma dispar) | 11.0 (± 0.9) | 3.9 (± 2.3) | 4.6 (17)| 0.01| 13 | - |
| Subtidal sponges (Spirastrella sp.) | 11.0 (± 0.1) | 10.4 (± 0.2) | 2.4 (31)| 0.02| 46 | - |
| Zooplankton*        | 11.3 (± 0.2)   | 10.9 (± 0.2) | 3.0 (5)| 0.03 | 46 | 6  |
the disintegration of ecologically important land to sea nutrient connections. Intense increases in nutrient inputs associated with human sewage and agriculture contributed to the collapse of the biologically, structurally, and interactively complex coral reef communities in Kaneoh Bay, Hawaii. Overfishing of salmon in the Pacific Northwest USA compromised the transfer of nutrients from marine to freshwater ecosystems affecting terrestrial plant and animal communities in a variety of ways.

While numerous other such examples exist, anthropogenic disturbances should not universally be expected to cause contractions in ecological interaction chain length or reductions in system connectivity. The character of the disturbance in question as well as the properties of the recipient system will both determine the final effects that human change has on networks of ecological interactions. However, because many sources of anthropogenic change have the effect of rapidly altering the overall and relative abundance of particular species, directly removing species, introducing species foreign to established ecological interaction networks, eliminating habitat, and changing the physical and chemical properties of local environments – we argue that human-induced contractions or eliminations of ecological interaction series are likely to have occurred and be occurring much more commonly than is presently appreciated.

Recognizing the effects on anthropogenic activities on ecological interaction chains is more difficult than documenting more tangible disturbance effects (e.g. species extinctions or introductions) because interactions between species and ecosystems do not fossilize and leave little material evidence behind to chronicle their disappearance. However, observations made in more-intact ecosystems, such as those reported herein, help bring these losses in interaction chain-length to light and highlight the implications that this type of environmental change may be having upon ecosystem connectedness. Sustained investigation of our remaining uniquely pristine environments will help to extend our understanding of the ubiquity and importance of this intangible, but potentially important type of shifting baseline.

Methods

Study Site. Data collection took place at Palmyra Atoll (8° 52′ N, 162° 04′ W; principally in the eastern lagoon basin) from 2009–2010. Palmyra is located in the Northern Line Islands in the central Pacific. The 12 km long atoll is composed of a series of small islets that are all composed of coral-derived materials. Islets encircle an intertidal saltwater lagoon system. The lagoons of Palmyra have been characterized as series of small islets that are all composed of coral-derived materials. Islets encircle an Northern Line Islands in the central Pacific. The 12 km long atoll is composed of a principally in the eastern lagoon basin) from 2009–2010. Palmyra is located in the

Comparisons of manta ray concentrations (used as a proxy for primary productivity) were monitored on a subset of transects by entraining known quantities of phytoplankton in transparent acrylic growth chambers fitted with 1 cm diameter polycarbonate membranes. Percent changes in Chl a were fluorometrically determined relative to starting concentrations after 3 days. Replica temporal measurements were made during the duration of the study of runoff water, zooplankton biomass, manta visual surveys, and Chl a concentrations (Table 1).

Isotopic analysis. To examine whether mechanistic ties existed between the components in this proposed interaction chain, we measured the δ15N isotope values of soils, tree leaves (T. argentea), intertidal clams (Macoma dispara), subtidal sponges (Sparisello sp.), and zooplankton in both native and palm forests transects/coastal areas (Thermo Finnigan Delta plus IRMS/Carlo Erba elemental analyzer).

Data analysis. Statistical comparisons between data collected in both forest types were analyzed using SPSS R. All analyses were compared using Welch t-tests or, when assumptions for parametric tests were not met, Wilcoxon nonparametric tests (manta point count surveys only).

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Author contributions

DJM, PAD, HSY designed and performed research, analyzed data, and wrote the paper. RBD, RD, MMM, and FM designed research, analyzed data, and wrote the paper.

Additional information

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