Coral skeletons reveal the history of nitrogen cycling in the coastal Great Barrier Reef

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Anthropogenic nutrient discharge to coastal marine environments is commonly associated with excessive algal growth and ecosystem degradation. However in the world’s largest coral reef ecosystem, the Great Barrier Reef (GBR), the response to enhanced terrestrial nutrient inputs since European settlement in the 1850’s remains unclear. Here we use a 333 year old composite record (1680–2012) of 15N/14N in coral skeleton-bound organic matter to understand how nitrogen cycling in the coastal GBR has responded to increased anthropogenic nutrient inputs. Our major robust finding is that the coral record shows a long-term decline in skeletal 15N/14N towards the present. We argue that this decline is evidence for increased coastal nitrogen fixation rather than a direct reflection of anthropogenic nitrogen inputs. Reducing phosphorus discharge and availability would short-circuit the nitrogen fixation feedback loop and help avoid future acute and chronic eutrophication in the coastal GBR.
The global anthropogenic production of nitrogen (N) is now equivalent to the amount of N generated through biological dinitrogen (N₂) fixation. Furthermore, human activity has more than doubled the pre-industrial input of N into the ocean. While there are many examples of nutrient input to coastal ecosystems leading to algal blooms and eutrophication, other systems show a mixed response, including resilience to such inputs.

Indeed the discharge of terrestrial nutrients and organic matter can accelerate N loss through microbial processes such as denitrification and anammox. In this case phosphorus (P), which is not lost through microbial activity, can accumulate leading to N limitation (i.e. low inorganic N:P ratios). In tropical systems N limitation can promote N₂ fixation, and this process acts to restore balance to the N:P ratio (Fig. 1a). The response of coastal ecosystems to nutrient enrichment therefore is not always a simple cause and effect relationship between nutrient availability and algal growth.

On the Great Barrier Reef (GBR), the world’s largest coral reef ecosystem, numerical estimates and coral skeleton proxy data clearly show that particulate and dissolved nutrient inputs have been increasing since European settlement in the 1850s. This has led to the conclusion that the coastal GBR is not only N replete, but probably eutrophic in some parts. But this is at odds with nutrient budgets for the modern coastal GBR that show strong N deficits (i.e. more N leaving the system than coming in). The discrepancy between N inputs and losses in the coastal GBR, and elsewhere, may simply be due to an over and underestimation, respectively, of rates of denitrification and N₂ fixation. However in the GBR there is other evidence to suggest that the apparent N deficit is not just a methodological artefact. For example, except during large flood events, concentrations of inorganic N (i.e. NO₃⁻ and NH₄⁺) are consistently low (<0.2 μmol L⁻¹) in coastal GBR waters. This may be explained by rapid uptake of inorganic N by phytoplankton, indeed the abundance of phytoplankton is thought to have increased in the coastal GBR as a result of terrestrial nutrient enrichment. However, increased phytoplankton abundance has been difficult to confirm against a backdrop of high seasonal variability in chlorophyll concentrations and a general lack of reliable long-term data. In any case, phytoplankton eventually settle and become incorporated into sediment organic matter, which is efficiently processed and subsequently lost via denitrification.

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**Fig. 1 Great Barrier Reef nitrogen cycle and study sites.** a Simplified conceptual model of nitrogen cycling in the coastal GBR. Terrestrial organic matter, P, and NO₃⁻ are transported by river runoff. The organic matter and NO₃⁻ in runoff fuels denitrification but P accumulates in the system. The low N:P ratio stimulates N₂ fixation which supplies low δ¹⁵N-N to coastal corals and subsequently decreases their skeletal δ¹⁵N. The δ¹⁵N of terrestrial N is higher than that derived from N₂ fixation. b Bathymetric map of the central GBR showing the location of Havannah Island and Pandora Reef (black circles). The Burdekin and Herbert Rivers, and the generalised direction of flood plume transport (black arrows) are shown. The location of a previous study (Magnetic Island) is also shown. The white numbered dots are the locations of flood plume and coastal water samples collected in March 2019 (sites 1-5), and November 2018 (sites 4-6), respectively. The dotted line encloses the area used to convert literature areal values of N₂ fixation into N loads per annum.
Denitrification is a major loss pathway for N in the coastal GBR and rates exceed N input through N2 fixation (ref. 26 and references therein). If enhanced terrestrial discharge is promoting greater denitrification then the preferential loss of N in coastal GBR sediments should manifest as an increase in P availability. This is supported by coastal water column and sediment nutrient concentration data, which consistently shows N:P ratios well below the Redfield ratio of 16:1.25,26,29,30,31, and below the average N:P of terrestrial runoff25. This has led to the supposition that other than during flood events, the GBR lagoon is N limited for most of the year26. Furthermore, nutrient budgets compiled by Furnas, Alongi et al. 26 also report that in the wet tropics region of the inshore GBR there is a surplus of P availability but a strong N deficit. This relatively high P availability in the coastal GBR should promote N2 fixation30. Indeed some of the earliest reports of water quality degradation in the GBR argued that N2 fixation has increased as a result of anthropogenic activity27,29. However the idea that N2 fixation has increased in the coastal GBR as a result of European activity has been contentious and difficult to prove without long-term (i.e. pre-European) records31,32. So how has N cycling in the coastal GBR responded to increased nutrient input since the 1850s, and how can we address this question without long-term records of N cycle process rates in the coastal GBR? Here, we use the 15N/14N (i.e. δ15N, where δ15N = [(15N/14N)sample/(15N/14N)air] − 1) of N trapped in the organic skeletal matrix of massive reef-building corals (hereafter called CS-δ15N) to understand how N cycling in the coastal GBR has responded to anthropogenic nutrient discharge since European settlement. The proxy-based approach relies on the fact that the δ15N of marine N, which is consumed by corals and recorded in their skeletons38–40, is an integrated signal of changes in N sources and availability. Greater N availability as a result of anthropogenic activity should have changed CS-δ15N to match the δ15N of terrestrial N impacted by fertiliser application and land-clearing. Such modifications can increase the δ15N of the residual N pool11–14, particularly when surface and groundwater systems are linked38,45. Furthermore, N enrichment can cause changes in microbial community composition, and coral physiology, that act to increase δ15N (see Table 1 in Erler, Wang et al.46). Therefore, anthropogenic N enrichment should have the net effect of increasing CS-δ15N. Alternatively, if N is being lost from the system through greater denitrification, then this should lead to enhanced N2 fixation, which would act to reduce CS-δ15N as nitrogen fixation reduces the δ15N of the water column N pool47–49.

For this study, we analysed CS-δ15N in four Porites lutea coral cores (2–3 samples per year) from two locations, Havannah Island and Pandora Reef, in the central inshore GBR (Fig. 1b). An additional short core from Geoffrey Bay (Magnetic Island) was also analysed to extend a previous coral record from the same reef46. As a way of constraining the δ15N of N in terrestrial runoff, we also measured the δ15N of N in coastal waters before and after a major flood event in 2019. The coral records show a long-term decline in the δ15N of the coastal nutrient pool towards the present. When combined with the water sample δ15N data, these trends suggest that N2 fixation has increased in the coastal GBR since European settlement.

Results and discussion

Long-term changes in coral skeleton nitrogen isotopes. The composite CS-δ15N records for Havannah Island and Pandora Reef (Fig. 2a, b) were significantly and positively correlated (r = 0.56, p < 0.001) during the 143-year period over which they overlapped (i.e. 1863–2005) and their long-term average CS-δ15N values were also similar (6.0 ± 0.7‰ and 5.8 ± 0.6‰, respectively). Shifts in CS-δ15N within each core therefore reflect ecosystem-level changes in external δ15N rather than physiological variability within the individual corals. First, we describe the long term changes in the CS-δ15N records before examining the reasons that may have caused these changes.

The patterns of CS-δ15N variability in corals from both reefs matched reconstructed Burdekin River flow derived from coral luminescence data39, indicating that river runoff led to increased CS-δ15N, and that dry periods led to decreased CS-δ15N (Fig. 2a, d). The correlations were generally better when short-term variability was excluded, and prior to 1940 (Supplementary Table 1). These relationships suggest that N enrichment following terrestrial runoff events increases CS-δ15N, supporting the notion that bulk terrestrial N has a relatively high δ15N, or that increased N availability increases water column N through trophic or metabolic interactions33. During dry periods CS-δ15N decreases, suggesting the increased contribution of N2 fixation to the inshore N pool. The increase in N2 fixation during dry periods has been observed in the modern GBR33 and fits the hypothesis that in the coastal GBR N can become limiting to the point where diazotrophs can outcompete other phytoplankton30.

Two lines of evidence suggest that the patterns in N cycling at the study sites have been altered by anthropogenic activity since the 1850s. Firstly, there is a significantly decreasing trend in CS-δ15N from 1680 to 2012 (Fig. 2a, b), and secondly there is a shift in the response of CS-δ15N to rainfall in the latter half of the 20th century that is not observed during pre-European wet periods (Fig. 3a, b). In the first 100 years of the Havannah Island record (1680–1780) the mean CS-δ15N was 6.4 ± 0.5‰, significantly higher (Student’s t-test, p < 0.001) than the last 100 years of the record (mean CS-δ15N of 5.8 ± 0.4‰). The mean CS-δ15N between 1940 and 2012 was lower still with a mean of 5.6 ± 0.4‰, representing a 0.8‰ decrease compared to the first 100 years of the record (double the analytical precision of the CS-δ15N method). In addition to changes in mean CS-δ15N, the Havannah Island record showed a significantly decreasing CS-δ15N trend (Mann–Kendall trend test, p < 0.001). The Pandora Reef record also had a significant negative trend in CS-δ15N between 1863 and 2012 (Mann–Kendall trend test, p < 0.001), and while this core does not capture the full extent of climatic variability evident in the Havannah Island record, it can still speak to the changes occurring in the latter half of the 20th century.

Notably, a similar decreasing trend in CS-δ15N was not recorded in a previous long core from Magnetic Island (1820–1987), some 60 km south of Havannah Island46. While the lack of change in CS-δ15N for the Magnetic Island core was used as evidence that there was no N enrichment in the coastal GBR as a result of European settlement46, the absence of a decreasing trend warrants further investigation. In the present study we updated the previously published Magnetic Island CS-δ15N record with a 25-year short core (1987–2011) from the same reef. A trend test over this new composite record revealed a significant decrease in CS-δ15N, but only between 1860 and 2011 (Fig. 2c). In the century before 1860 the central inshore GBR experienced lower than average river runoff (Fig. 2d), which according to the Havannah Island record, resulted in a prolonged decrease in CS-δ15N (Fig. 2b). Such a decrease suggests a period of severe N limitation and a greater reliance on N2 fixation. Because the Magnetic Island record does not capture the wetter period prior to 1780, we started the trend test from 1860 and not 1820.

The timing of the decrease in CS-δ15N in the updated coral record for Magnetic Island is also later than in the Pandora Reef and Havannah Island records. This may in part be due to the removal of the impacts of dredge spoil on Magnetic Island corals, which may have been masking any decrease in CS-δ15N. Coral
communities on Magnetic Island have been exposed to dredge spoil since the 1880s, but significant efforts to improve the management of dredge spoil discharge only began in the 1990s. Alternatively, the stability of the Magnetic Island record between 1820 and 1987 may be due to the antagonistic effects of increased δ15N in terrestrial N runoff (higher CS-δ15N) and higher rates of coastal N2 fixation (decreased CS-δ15N) (see discussion below). Given the proximity of Magnetic Island to the Burdekin River, it may be more influenced by high terrestrial N than the two reefs further north. In any case, taken together, all three coral records from the same coastal region of the GBR suggest a decrease in CS-δ15N in the latter half of the 20th century.

In addition to this long-term decreasing trend in CS-δ15N, the Havannah Island and Pandora Reef coral records also show a shift in the relationship between CS-δ15N and Burdekin River flow between 1860 and 2012. Between 1860 and 1940 CS-δ15N and Burdekin River flow anomalies are positively correlated, with peak river flow corresponding with increased CS-δ15N and vice versa (Fig. 3a, b). For the Havannah Island core, these correlations are mostly significant. After 1940, both the Havannah Island and Pandora Reef CS-δ15N records are poorly, or inversely, correlated with Burdekin River flow anomalies (Fig. 3a, b). A similar pattern of poor and/or inverse correlation between CS-δ15N and Burdekin River flow anomalies can also be seen between 1770 and 1850 in the Havannah Island record (Fig. 3b), but this is a particularly dry period with mostly below average river flow (Fig. 2d). Between 1680 and 1770 the average Burdekin River flow anomaly is close to the long-term average (i.e. ~0 km³) and there is a positive correlation between CS-δ15N and Burdekin River flow anomalies, just like the period between 1860 and 1940. Therefore, the period between 1940 and 2012 stands out from previous periods of comparable Burdekin River runoff.

This is confirmed with change point analysis which shows an increase in the number of CS-δ15N minima after 1940 in both the Havannah Island and Pandora Reef records, and a reduction in the magnitude of the positive change points after
the complex modifications in isotope abundances that can occur in agricultural systems, particularly when surface and groundwater are linked\textsuperscript{58,45}, like they are in the Burdekin River catchment. We propose that the $\delta^{15}\text{N}$ of terrestrial N reaching the coastal GBR is likely to be higher than the $\delta^{15}\text{N}$ of N in soils, and that even though fertiliser N may have a low $\delta^{15}\text{N}$, by the time this N has moved through the landscape its $\delta^{15}\text{N}$ has been significantly altered by biological processing.

To constrain the $\delta^{15}\text{N}$ of modern-day terrestrial N reaching the central inshore GBR we compared the $\delta^{15}\text{N}$ of the total dissolved N pool ($\delta^{15}\text{N-TDN}$) before and after a major flooding event (Supplementary Fig. 1) in the central inshore GBR (Sites 1–6 in Fig. 1). Total dissolved N is a mix of terrestrial dissolved organic N (e.g. from soils), dissolved organic N released from particulate N in the water column, and dissolved inorganic N from surface/groundwater sources. The $\delta^{15}\text{N-TDN}$ therefore integrates the $\delta^{15}\text{N}$ of the different N pools in terrestrial discharge or coastal waters, and also captures the isotopic fractionation that occurs during N transformation between the pools (Supplementary Fig. 2). As confirmation of this we measured the $\delta^{15}\text{N}$ of particulate material before the flooding event (Sites 4–6), finding that it was within 0.5‰ of the $\delta^{15}\text{N-TDN}$ at the same sites (Supplementary Table 2). As such, the $\delta^{15}\text{N-TDN}$ should be a good representation of the $\delta^{15}\text{N}$ of N available to coastal corals.

The measured $\delta^{15}\text{N-TDN}$ in the Burdekin River flood plume (March 2019) ranged from 6.2±0.1‰ at the river mouth, to 4.6±0.6‰ at Site 6 (Supplementary Table 2). Prior to the flood event (November 2018) the average $\delta^{15}\text{N-TDN}$ at Sites 4–6 was 4.1±0.7‰ (Supplementary Table 2). The flood plume sampling occurred about a month after the main discharge event, which means there would already have been significant mixing of coastal water with river runoff. To determine the $\delta^{15}\text{N-TDN}$ of the terrestrial endmember, we used an isotope mixing model of measured concentrations and $\delta^{15}\text{N}$ in water samples collected before and after the flood event (see Supplementary Note 1). With this approach the $\delta^{15}\text{N-TDN}$ of terrestrial N was calculated to be 8.1±1.1‰. This is higher than the $\delta^{15}\text{N}$ of catchment soils\textsuperscript{55} and of fertiliser N\textsuperscript{54}. In general CS-$\delta^{15}\text{N}$ is up to 2‰ higher than its N source, so given that the average CS-$\delta^{15}\text{N}$ was 5.6‰ between 1940 and 2012, the $\delta^{15}\text{N-TDN}$ of terrestrial N would need to be between 3.6‰ and 5.6‰ if it was to be the dominant source of N for corals in that period.

Based on our rather limited assessment, it would appear that the calculated $\delta^{15}\text{N}$ of terrestrial N is too high for it to have caused the decreases in CS-$\delta^{15}\text{N}$ observed in the coral records. Other studies also support the idea that the $\delta^{15}\text{N}$ of terrestrial N has increased with increased application of N to adjacent farming land. For example, the $\delta^{15}\text{N}$ in terrestrial material recovered from a Magnetic Island coral skeleton\textsuperscript{46} increased from 2.5‰ to 9.5‰ between 1820 and 1987. Another study measured the $\delta^{15}\text{N}$ of acid insoluble material (which is effectively terrestrial N) in coral skeletons from the southern coastal GBR, finding values of around 8.5‰, and as high as 13.6‰, during flood events\textsuperscript{56,57}. These same studies reported $\delta^{15}\text{N}$ values of particulate N in catchment runoff of up to 9.5‰. Unfortunately there are very few studies reporting the $\delta^{15}\text{N}$ of terrestrial N reaching the coastal GBR, but the evidence both from our study and others support the idea that the $\delta^{15}\text{N}$ of terrestrial derived N is too high to be the driver of reduced CS-$\delta^{15}\text{N}$ observed in the coral records from the central inshore GBR.

The other possible driver of reduced CS-$\delta^{15}\text{N}$ in the Havannah Island, Pandora Reef, and Magnetic Island coral records is N\textsubscript{2} fixation. To try and quantify the amount of N entering the coastal GBR through N\textsubscript{2} fixation we developed a second isotope mixing model (see Supplementary Text 2 for a full description). The model assumes that the N available for consumption by coastal

**Fig. 3** Coral skeleton CS-$\delta^{15}\text{N}$ and Burdekin River flow correlation plots. a Correlation coefficients for a moving correlation (30-year window) between the annual Pandora Reef CS-$\delta^{15}\text{N}$ record and Burdekin River flow. Red dots show significance at the 95% level. b Correlation coefficients for a moving correlation (30-year window) between the annual Havannah Island CS-$\delta^{15}\text{N}$ record and Burdekin River flow. Red dots show significance at the 95% level. c Change points for Pandora Reef (green) and Havannah Island (blue) composite CS-$\delta^{15}\text{N}$ records. Change point values are normalised to the overall mean CS-$\delta^{15}\text{N}$ of each core.

1940 (Fig. 3c). The sum of our evidence therefore suggests that the CS-$\delta^{15}\text{N}$ is lower after 1940 than during any other previous period of comparable river flow.

**Reasons for decreased CS-$\delta^{15}\text{N}$ in the inshore GBR.** The decrease in CS-$\delta^{15}\text{N}$ in the latter half of the 20th century implies that a new source of N with a lower $\delta^{15}\text{N}$ has been added to the coastal GBR N budget. The two possible sources are N\textsubscript{2} fixation, or terrestrial N that has been modified by the addition of fertiliser (which can have a low $\delta^{15}\text{N}$). Rainfall is included as a terrestrial source as it deposits atmospheric N back on land which then flows to the coastal GBR. For the Burdekin River catchment the $\delta^{15}\text{N}$ of undisturbed forest soils is ~6.3‰, however modified soils in the modern Burdekin River catchment have an average $\delta^{15}\text{N}$ of ~5.8‰, possibly reflecting the addition of artificial fertilisers since the 1930s\textsuperscript{55}. Therefore, the observed decreases in CS-$\delta^{15}\text{N}$ in the coral records could simply be attributed to an increase in the amount of fertiliser used in the Burdekin River catchment, since European settlement (which decreases the $\delta^{15}\text{N}$ of terrestrial N). However, directly linking CS-$\delta^{15}\text{N}$ with terrestrial $\delta^{15}\text{N}$ ignores
carnals comes from both terrestrial N inputs (measured as δ¹⁵N-TDN, see above) and N₂ fixation. The average CS-δ¹⁵N value between 1940 and 2012 for the Havannah Island coral was used to determine the contribution of these two sources to the coastal N pool (after accounting for fractionation between the coral and the N source). Outputs from the mixing model show that between 1940 and 2012, the minimum and maximum possible contributions of N₂ fixation to the inshore N pool are 17% and 55% (Fig. 4). Using the average δ¹⁵N-TDN value for the flood plume waters of 8.1‰, and accounting for fractionation during uptake of N by corals, N₂ fixation was constrained to within 27% and 50% of annual N inputs at the study site (Fig. 4).

While our data shows that the proportional contribution of N₂ fixation to the coastal N pool has increased with anthropogenic inputs, it cannot tell if the rate of N₂ fixation has increased. For instance, if terrestrial N is being preferentially lost after discharge, then the N from N₂ fixation may make up a larger fraction of the coastal N pool without the rate of N₂ fixation actually increasing over time. To convert the fractional contributions into actual amounts of N entering the system through N₂ fixation, we used the modelled terrestrial N input values of Waters, Carroll et al. 14 for the Burdekin and Herbert Rivers (Supplementary Note 3). We estimate that the average annual input of N from N₂ fixation to the central inshore GBR between 1940 and 2012 ranged between 2073 and 11,897 tonnes yr⁻¹, with an average value of 6808 tonnes yr⁻¹ (Fig. 4). This is the same order of magnitude as N₂ fixation estimates from Furnas, Alongi et al. 26 (3225 tonnes yr⁻¹), which includes water column and sediment rates), the range of values reported by Bell, Elmetri et al. 58 (average of 3311 tonnes yr⁻¹, water column rates only), and the estimates of Messer, Brown et al. 31 (6332 tonnes yr⁻¹, water column only). Note that our estimate of N₂ fixation is calculated as a proportion of the annual terrestrial N load debouched by the Burdekin and Herbert Rivers, whereas the reported literature rates are up-scaled from areal or volumetric rates (see Supplementary Note 3 for a description of the scaling procedure). Furthermore, the literature values relate to coastal regions that may not include our study site. Nevertheless, the similarity between our rates and literature values provides some vindication of our model calculations.

Next we calculated the annual rate of N₂ fixation in the first 100 years of the record. This period was selected because it is the only interval prior to European settlement that has comparable, albeit lower, rainfall to the modern GBR. To perform the mass balance calculation we used the same mixing model as for the modern GBR, but adjusted the CS-δ¹⁵N to match the average value between 1680 and 1780 (i.e. 6.4‰). We assumed that the δ¹⁵N of terrestrial discharge (δ¹⁵N-TDN) was the same as the modern GBR (i.e. between 7‰ and 9.2‰), which actually overestimates the pre-European rate (because δ¹⁵N-TDN was probably lower). Similar to the calculation for the modern GBR, we used published estimates of annual terrestrial N inputs prior to European settlement 14 to deduce a value for N produced through N₂ fixation (Fig. 4).

The average modelled estimate of N₂ fixation for the central inshore GBR between 1680 and 1780 was 2094 tonnes yr⁻¹ (green line in Fig. 4). This is lower than estimates for the modern GBR (red lines in Fig. 4). Even acknowledging the wide range in the N₂ fixation estimates, it appears likely that the quantity of N imported into the coastal GBR has increased since pre-European times. This represents the first evidence that N₂ fixation in the coastal GBR is higher now than prior to European settlement. We hypothesise that increased terrestrial runoff has increased denitrification and decreased the N:P of the coastal GBR since European settlement. This in-turn has manifested as an increase in the amount of N₂ fixation now occurring in coastal waters.

Implications for coastal nutrient management in the GBR.
Studies on N₂ fixation conducted in the early 1990s reported increased rates in the coastal GBR relative to the 1930s22,23. The increase in N₂ fixation was thought to import new N and organic matter into the system, potentially stimulating inorganic N availability and enhanced primary production. As such, the observed increases in N₂ fixation were used as evidence that the GBR was heading towards widespread eutrophication. However, assessments of coastal primary production, paleo-reconstructions, or large-scale N budgets for the GBR do not support this26,34,59. Nevertheless, these early N₂ fixation studies do raise a crucial point, what will happen to the new N imported into the coastal GBR through enhanced N₂ fixation? From a benthic biogeochemical perspective, an increase in organic N delivery to sediments following N₂ fixation is likely to fuel sediment anoxia and enhance denitrification, perpetuating N limitation. As P continues to accumulate, eventually the amount of N entering through N₂ fixation will overwhelm the denitrification capacity of the system, at which point water column DIN availability will increase and classical eutrophic conditions may take hold. Current estimates show that denitrification rates exceed N₂ fixation rates in the inshore GBR26, but it is not clear how long this will persist. While much of this discussion is speculative, it does highlight the importance of reducing terrestrial P discharge to the coastal GBR. Our data suggests that reducing terrestrial P discharge and availability would short-circuit the N₂ fixation feedback loop and help avoid future acute and chronic eutrophication in the coastal GBR.

Methods
Study sites and sample details. Porites lutea coral cores from Havannah Island, Pandora Reef, and Magnetic Island (Geoffrey Bay) were selected from the Australian Institute of Marine Sciences Coral Core Archive. The Havannah Island cores cover the period from 1680 to 2012, and the Pandora Reef cores spanned
from 1863 to 2005. As such this the CS-δ15N record is sufficiently long to separate the influence of changing rainfall patterns associated with the end of the Little Ice Age
and the onset of global warming48, from the effects of local anthropogenic activity on N dynamics in the central inshore GBR. The chosen reef systems lie between the Burdekin and Herbert Rivers which are ranked 1 and 3, respectively, in terms of average annual freshwater discharge to the GBR25. The selected inshore reefs are are considered to be relatively unaffected by oceanic upwelling from the Coral Sea. Therefore, while our study is based on only one small region of the GBR, the coral collection sites are sandwiched between these two large river systems and our findings are broadly applicable to other high input inshore regions of the GBR. One long core (>100 years old) and one shorter core (<50 years old) from Havanah Island and Palfrey Reef were selected for analysis from the ALSM coral core archive (core details are given in Supplementary Table 3). One short core was selected from Geoffrey Bay (Magnetic Island) to extend a previous coral record from the same reef49. Coral carbonate powders (~100 mg) were collected from ultrasonically cleaned skeletal slabs using a small drill and a 2 mm diameter carbide engraving bit along the central growth axis. Samples were collected from each high and low density band (i.e. two samples per year of growth). Where annual skeletal extension was >10 mm, additional samples were collected from the low density bands (i.e. minimum of two and maximum of three samples per year of growth). The ages of the skeletal bands were based on previous chronologies of the same cores61,62.

**Analysis details.** Following collection, skeletal powders were grounded with an agate pestle and mortar (to <63 μm) and transferred to a 15 ml centrifuge tube for chemical cleaning with ultrapure NaClO bleach. The detailed method for obtaining intra-crystalline CS-δ15N from cleaned coral skeletal material is based on the persulfate oxidation of liberated organic material to NO3−11 and subsequent measurement of its δ15N after conversion to N2O51. Analysis of the δ15N-N2O produced from the coral powders was performed with a Thermo Delta V Plus Isotope Ratio Mass Spectrometer (IRMS). Nitrous oxide was concentrated with a custom built purge and trap system coupled to the IRMS via a Thermo GasBench II interface. All CS-δ15N analyses were performed in triplicate and the analytical precision was 0.4‰. Water samples from the 2018/2019 Burdekin River flood plume, collected by AIMS staff, and water samples from Sites 4 to 6 (November 2018), were collected from 1 and 5 m depth at each site using a Niskin water sampler. All water samples were analysed for total dissolved nitrogen concentration (flow injection analysis), and the δ15N of total dissolved nitrogen63,64. The CS-δ15N and N content of particulate N trapped on pre-combusted glass fibre filter paper was determined on samples (8–24 L) collected from Sites 4 to 6 (November 2018). Analysis was performed on an elemental analyser coupled to an IRMS.

Trend analysis was performed with the Mann–Kendall trend test69 after the composite CS-δ15N record (i.e. combined raw data from both cores at each site) had been discretised into 0.5 year bins. Comparisons of mean CS-δ15N between different time periods was done with Student’s t-test. Change point analysis was used to identify abrupt increases or decreases in the composite discretised (0.5 year bins) CS-δ15N records. The minimum threshold (i.e. the minimum improvement in total residual error for each change point) was set to 0.4. Change point analysis calculates the period over which a significant change occurs and the mean CS-δ15N over this period was selected as the changepoint value. Change point values were normalised on a long-term mean in each composite record (i.e. a negative change point represents a decrease relative to the long-term mean).
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Acknowledgements
This work was supported by an Australian Research Council Discovery Project grant (DP170100734). We would like to thank E. Matson (AIMS) for assistance with core sampling, and R. Gruber and B. Robson (AIMS) for supplying the flood plume water samples. I. Alexander and M. Carvalho (SCU) were involved in laboratory analysis, and A. McMahon and S. Rogan were involved in water sample collection.

Author contributions
D.V.E., H.T.F., T.D.G., and N.L.C.-P. were responsible for coral sampling. J.M.L. coor-dinated access to the AIMS coral archive. Samples were analysed by H.T.F. and D.V.E. The manuscript was written by D.V.E. in collaboration with all authors.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary information is available for this paper at https://doi.org/10.1038/s41467-020-15278-w.

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Peer review information Nature Communications thanks Michelle Devlin, Chris Langdon, and other, anonymous, reviewer(s) for the contributions to the peer review of this work.

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