Estimating N release from climate warming

Assuming that (1) annual heterotrophic respiration in unmanipulated tundra is roughly equal to total plant production ($150\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) as it is in many mature ecosystems, (2) that soil respiration responds to temperature change with a Q_{10} of 2, and (3) the depth-weighted average C:N ratio of SOM is 26 (Supplementary Information), then the projected 3 °C temperature increase[1] should result in the mineralization of $7\,\mathrm{g\,N\,m^{-2}\,yr^{-1}}$. A 7 °C temperature increase should result in the mineralization of $9.4\,\mathrm{g\,N\,m^{-2}\,yr^{-1}}$. This is a conservative estimate of temperature stimulation of N release because respiration in soils from cold regions tends to be highly sensitive to temperature, often responding to temperature change with Q_{10} values greater than 2 (ref. 30). Nevertheless, these simple calculations show that our rate of N addition is similar in magnitude to potential N release from climate warming.

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Environmental predictors of pre-European deforestation on Pacific islands

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Some Pacific island societies, such as those of Easter Island and Mangareva, inadvertently contributed to their own collapse by causing massive deforestation[1–7]. Others retained forest cover and survived[3,8,9]. How can those fateful differences be explained? Although the answers undoubtedly involve both different cultural responses of peoples and different susceptibilities of environments, how can one determine which environmental factors predispose towards deforestation and which towards replacement of native trees with useful introduced tree species? Here we code European-contact conditions and nine environmental variables for 81 sites on 69 Pacific islands from Yap in the west to Easter in the east, and from Hawaii in the north to New Zealand in the south. We thereby detect statistical decreases in deforestation and/or forest replacement with island rainfall, elevation, area, volcanic ash fallout, Asian dust transport and makatea terrain (uplifted reef), and increases with latitude, age and isolation. Comparative analyses of deforestation therefore lend themselves to much more detailed interpretations than previously possible. These results might be relevant to similar deforestation-associated collapses (for example, Fertile Crescent, Maya and Anasazi) or the lack thereof (Japan and highland New Guinea) elsewhere in the world.

All Pacific islands suitable for agriculture were occupied before European arrival by colonists originating ultimately from Asia, mostly in a wave of Polynesians and their Lapita ancestors from 1200 BC to AD 1200 (refs 2, 10, 11). They cleared land and cut trees, especially for agriculture, timber and fuel. Early European visitors observed that forest cover varied greatly between islands, from totally deforested with almost all original tree species extinct (Easter, Necker and Nihoa) to extensive forests (Samoa, Taveuni and Bismarck Archipelago). Forests seen by early Europeans also varied greatly in composition, from ones still dominated by native species to others whose native species had been largely replaced by introduced species valuable for arboriculture.

From accounts of early European visitors, we coded five-point scales for deforestation (in which 1 represented virtually no deforestation and 5 complete deforestation) and for forest replacement (in which 1 represented virtually no replacement and 5 complete replacement) (see Methods and Supplementary Table S1 for details). Deforestation and replacement proved to be correlated, but they measure different things and the correlation is not tight (Spearman correlation $r = 0.43$, $p < 0.001$, in our data set of 81 entries). For 12 of our 69 islands we coded two different locations on the island (usually windward and leeward coasts) because of very different rainfall values often associated with different degrees of deforestation. Thus, our full data set had $69 + 12 = 81$ entries. We also analysed a reduced data set of 69 entries, which excluded 12 large islands of northern Melanesia and New Zealand, because we wondered whether those 12 islands might be driving some conclusions, but results were similar.

We performed four types of statistical analysis (see Methods) for both data sets, relating our two outcome variables (deforestation and replacement) to nine independent variables discussed below.

The first statistical analysis was the calculation of bivariate Spearman correlations (Supplementary Tables S2–S6), and the corresponding bivariate regression coefficients, among the two outcomes and the nine independent variables. The second analyses were multivariate regression analyses[12], to take account of correlations among the independent variables. The third were multivariate tree models to divide the data, by recursive binary partitioning based on potentially more than one independent variable, into groups each homogenous in outcome value within the group but maximally contrasting in outcome value between groups[13]. Unlike multivariate analysis, this approach seeks sets of explanatory variables that might interact conditionally instead of acting independently. The last analysis was the examination of residuals (actual values minus model-predicted values) from the best-fit multiple regression and tree models, to identify data points fitted poorly by the models and thereby suggesting other explanatory factors besides those incorporated into the models.

Tables 1 and 2 summarize the results of the first three types of statistical analysis. (Conclusions drawn from residuals are mentioned in the text below.) Signs of significant effects were mostly consistent between the analysis types. Effects on deforestation and on forest replacement had the same sign for six independent variables and opposite signs for one variable (latitude), whereas makatea and dust significantly affected forest replacement but not deforestation.

We now explain each independent variable whose possible role we had proposed at the outset, and the results for that variable. Two variables—rainfall, and latitude as a surrogate for temperature— were chosen because rainfall and temperature are primary determinants of plant growth rates. We reasoned that deforestation

should be less severe in areas where tree regrowth rates can keep pace with logging rates. A third variable, makatea, was chosen for reasons given below. Three variables—island age, volcanic ash fallout and Asian dust fallout—were proposed to influence soil nutrient levels; regrowth is rapid on nutrient-rich soils (but those are also the soils preferred by farmers). The remaining three variables— elevation, area and distance—were proposed to have multiple indirect effects.

High rainfall was inversely associated with deforestation in all analyses (Table 1), and with replacement in one analysis (Table 2). That is, dry islands were more likely than wet islands to end up deforested. On 8 of the 12 islands for which we separately coded two locations, one location was much drier and also more deforested than the other, thereby offering a controlled natural experiment within an island. These effects are as expected; rainfall is often the most important single determinant of plant growth rates. In addition, low rainfall increases forest vulnerability to fire and hence to the formation of deforested grassland and fernland[14].

Deforestation increased with latitude in all analyses, as expected from the decrease in temperature and hence in plant growth rates with latitude. In contrast, forest replacement decreased with latitude, undoubtedly because two of the most important introduced trees (breadfruit and Tahitian chestnut) are tropical species whose cultivation decreases with latitude.

Parts of 7 of our 69 islands consist of a terrain called makatea. This uplifted reef formation of sharp, fissured coral bears little soil and is painfully difficult to walk on. Not surprisingly, all seven islands provide controlled natural experiments: makatea terrain retained forests, whereas non-makatea terrain became deforested. Our statistical analysis therefore showed low forest replacement

Table 1 Significant predictors of deforestation

Independent variable	Bivariate regression		Multivariate regression			Tree	
	81	69	81, A	69	81, no A	81	69
Rainfall (log)	−1.9***	−1.6***	−1.3***	−1.3***	−1.03**	−, 1	−, 3
Latitude	+0.066***	+0.092***	+0.034**	+0.07***	+0.03*	+, 2	+, 1
Makatea							
Age	+0.53†	+0.53†		+0.29†			+, 2
Tephra	−0.46***	−0.37***	−0.61†		−0.79*	−, 3	
Dust							
Elevation (log)	−0.42*	−0.25†		−0.45**	−0.46**		
Area (log)	−0.31**	−0.24†	−0.26***				−, 2
Distance (log)			+0.22***	+0.18†	+0.20†		−, 3
Variance accounted for			0.62	0.75	0.59	0.65	0.72

The Methods section explains the nine independent variables and the bivariate regression, multivariate regression and multivariate tree analyses. Numbers in the two bivariate columns are bivariate regression coefficients; numbers in the multivariate columns are the corresponding multivariate regression coefficients. The signs in the tree columns are the sign of the relationship between deforestation and that independent variable; numbers in the tree columns denote the sequence in which predictor variables enter the tree (earlier-entering predictors, with lower numbers, are more important). Levels of statistical significance are as follows: ***, $P < 0.0001$; **, $P < 0.001$; *, $P < 0.01$; †, $P < 0.05$. Cells left blank failed to reach significance at $P < 0.05$. We used as alternatives a full data set of 81 entries and a reduced data set with 69 of those entries (numbers '81' and '69' in the first row). Multivariate regression of the full set with all nine independent variables (81, A) was repeated after dropping area as an independent variable (81, no A); that repetition was unnecessary for the 69-entry set because area proved not to be a significant predictor of deforestation in that set.

Table 2 Significant predictors of forest replacement

Independent variable	Bivariate regression		Multivariate regression				Tree	
	81	69	81, A	69, A	81, no A	69, no A	81	69
Rainfall (log)	−0.45†							
Latitude			−0.03**	−0.03*	−0.04***	−0.03†		
Makatea			−1.0†		−1.88***	−1.45**		
Age	+0.49*	+0.56***	−0.27*	+0.27†	−0.32*	−0.21‡		
Tephra	−0.58***	−0.34***	−0.72***	−0.48***	−0.94***	−0.74***	−, 2	−, 2
Dust	−0.003***	−0.002***	−0.002***	−0.001‡	−0.002***	−0.002**		
Elevation (log)	−0.84***	−0.45***	−0.58†	−0.28†	−1.2***	−0.96***		
Area (log)	−0.63***	−0.43***	−0.28*	−0.27*			−1, 2	−, 1
Distance (log)			+0.18*	+0.15†	+0.15†	+0.12§		
Variance accounted for			0.86	0.73	0.84	0.73	0.74	0.67

As Table 1, but for forest replacement instead of deforestation. Levels of statistical significance are as follows: ***, $P < 0.0001$; **, $P < 0.001$; *, $P < 0.01$; †, $P < 0.05$; ‡, $P = 0.06$; §, $P = 0.07$. Cells left blank failed to reach significance at $P < 0.05$.

444

NATURE | VOL 431 | 23 SEPTEMBER 2004 | www.nature.com/nature

associated with makatea, which is difficult to use for arboriculture. Our first three types of statistical analysis failed to show a significant association between makatea and deforestation, probably because the signal from just seven islands was too weak to emerge statistically in the whole data set. However, that association did appear in our statistical residuals: two of our islands with the highest percentage of makatea (Makatea Island and Niue) had the highest or nearly the highest negative residuals in both the multiple regression and tree analyses; that is, they were less deforested than expected just from effects of our other independent variables.

Island or terrain age is relevant because soil nutrients become lost from volcanic surfaces with time, especially by rain leaching[15,16]. This effect, too, emerges from controlled natural experiments within islands: on Easter Island the oldest surface, the Poike Peninsula, became deforested several centuries before the younger remainder of the island[7]. In our statistical analyses deforestation increased with age, but the relation of forest replacement to age was inconsistent.

Those lost soil nutrients might become restored in three ways: volcanic ash fallout (aerial tephra), continental dust fallout and nesting seabird guano. The so-called Andesite line divides Pacific islands geographically into two groups: those whose volcanoes eject tephra carried by winds for up to 1,000 km and those whose volcanoes instead release lava with little aerial tephra. We did not realize this effect when we began our project, and it provided the biggest surprise: islands west of or near the Andesite line (that is, in or near the zone of aerial tephras) emerged with lower deforestation and forest replacement in all our types of non-residual statistical analyses.

Soil nutrients are also replenished by dust carried eastwards in the atmosphere from Central Asia[15–17]. That dust fallout declines eastwards and southeastwards in the Pacific. Forest replacement decreased with increasing dust fallout. (We suspect a role of correlated geographical factors rather than of dust itself.) We could not detect an effect of dust on deforestation, but it might help to explain why our two islands farthest from Central Asia and hence with the lowest dust fallout, Easter and Mangareva, had among the largest positive residuals from our multiple regression model (that is, more deforested than predicted by our best-fit model).

Elevation was inversely associated with deforestation and forest replacement: high islands supported more forest and more native trees than low islands. This effect also emerges from natural experiments: virtually all high islands are forested with native trees at high elevation, even if they are deforested or support mainly introduced trees at low elevation. At least four factors are probably involved: orographic rain is generated at high elevations, descends in streams and thus makes the lowlands effectively wetter than indicated by lowland rainfall; nutrients and soil eroded at high elevation are similarly carried in streams to the lowlands; orographic rain captures atmospheric dust; and agriculture (hence land clearance) decreases with elevation because of cool temperatures (unfavourable for tropical crops), steep slopes and difficult access.

Area was inversely associated with deforestation and forest replacement: large islands retained more forest and more native tree species than small islands. Multiple factors probably contribute, including the fact that larger islands have greater habitat and tree species diversity (hence higher likelihood of some species being spared from logging), tracts of inaccessible land, and lower perimeter/area ratios (hence fewer coastal resources to support human population).

Distance (isolation from other islands) was positively associated in multiple regression analyses with deforestation and forest replacement, which tended to be most severe on remote islands. Reasons might include people on islands near other islands having the options of emigrating, trading or raiding instead of staying at home and having an impact on the forests, and low diversity in tree species on remote islands decreasing the likelihood of any tree species being spared.

We can now reconsider why Easter Island[4] suffered almost the most extreme deforestation and consequent social and population collapse of any Pacific island, even though the Polynesians who colonized Easter colonized hundreds of other islands without wreaking such extreme impacts. Our study suggests part of the answer to be Easter's extreme environmental fragility predisposing towards deforestation: of our 69 islands, it has the lowest tephra and dust fallout, the second greatest isolation and third highest latitude and no makatea, and is relatively low, small and dry. On the basis of those independent variables, our multiple regression and tree models predict correctly that Easter should have the third highest deforestation score, exceeded only by Necker and Nihoa, which also ended up completely deforested. That is, Easter's collapse was not because its people were especially improvident but because they faced one of the Pacific's most fragile environments.

Finally, we note seven avenues for refining our analysis. First, effects of island age, tephra fallout and dust fallout interact in a complex manner with rainfall: for example, nutrient leaching with age, and hence nutrient replenishment by tephra or dust, should be more significant on wetter islands[16]. Second, our measures of tephra, dust and age should be refined. Third, we lack a measure of nutrient inputs in seabird guano. Fourth, large-scale deforestation in the continental moist tropics can reduce convection and rainfall and thus cause positive feedback on the initial deforestation rate, but it is uncertain whether the same cycle operates on small islands. Fifth, a possible role of time since first colonization should be reconsidered; our preliminary analysis failed to detect a role. Sixth, although we have examined contributions of environmental differences to differences in deforestation and replacement, social differences surely also contribute, as Kirch discussed[3]. Indeed, our residual analyses suggest this conclusion: Tikopia and Tonga, whose societies Kirch noted as employing especially effective protective measures against deforestation, had two of the most negative residuals unexplained by our regression equations based solely on environmental factors, whereas Mangareva—cited by Kirch to illustrate ineffective social measures—had one of the highest positive residuals. Easter also had a high positive residual, which might reflect social pressures driving deforestation for transporting its famous stone statues. Last, our analysis could be extended to other societies, elsewhere in the world, noted either for deforestation or lack thereof; we think that we can discern straightforward extensions to the Anasazi, Japan, highland New Guinea, the Fertile Crescent and other cases[1,6,8,9]. □

Methods

Values of the variables

The variables used are shown in Supplementary Table S1. Deforestation was scored on a five-point scale. A score of 1 represented no deforestation (no examples in our database; sole Pacific examples are some islands abandoned long ago or never settled by humans). A score of 2 meant densely forested; primary forests at higher elevation or on very steep slopes; mainly secondary forests with some introduced species at low elevations; no fire-associated vegetation. A score of 3 was as for 2 but with mainly introduced species in lowland secondary forests; much fire-associated grassland/fernland on ridges, slopes, and plateaus. A score of 4 indicated largely deforested; forests mainly on coastal plain, valley floors, and very steep slopes; fire-associated grassland/fernland covering all ridges and most slopes and plateaus. A score of 5 represented almost completely deforested; fire-associated grassland/fernland covering almost all areas not used as cropland.

Forest replacement was also scored on a five-point scale. A score of 1 indicated that introduced tree species comprised less than 10% of all tree individuals; 2, introduced tree species comprised 25–50% of forest tree individuals up to 600 m and less than 10% above 600 m; 3, introduced tree species comprised 50–75% of forest tree individuals up to 600 m and less than 10% above 600 m, with less land above 600 m than islands with a score of 2; 4, as 3 but introduced tree species comprised 75–100% of forest tree individuals up to 600 m; 5, there were few trees, and forest was mostly replaced by grasses and shrubs.

Sources for assessing deforestation and forest replacement were the earliest available first-hand descriptions by European visitors to each island (usually in the early-contact period), supplemented by paleoecological studies (pollen analysis).

We began with two alternative values for A (area) and D (distance): A of the individual island, or of all islands within 50 km; and D to nearest high island whose area is more than

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25%, or more than 75%, of *A* of the target island. We then discarded the second measure in each case because of its high correlation with the first measure ($r = 0.94$ for the *A* measures; $r = 0.66$ for the *D* measures).

Lowland rainfall values were taken from atlases, journal articles, technical reports and other sources. Windward and leeward coasts were coded separately on 12 islands.

Our data table lists latitudes of island midpoints north or south of the Equator, but initial analyses showed no differences between effects of latitudes north or south; our subsequent analyses therefore used the absolute value of latitude without regard to whether north or south.

Makatea surface area as a percentage of total island surface area was estimated from geological maps.

Ages of volcanic rocks on islands were coded as follows: 1, young (less than 20,000 yr old); 2, intermediate (20,000–1,000,000 yr old); 3, old (more than 1,000,000 yr old); X, no exposed volcanic rock. These cutoffs were chosen on the basis of rates of nutrient leaching from volcanic rocks[16]. Islands formed from mosaics of terrains of different ages were assigned average values: for example, old islands with some young lava flows were scored $(3 + 1)/2 = 2$. Sources were journal articles based on K–Ar dating of volcanic rock.

Aerial tephra fallout was scored as follows: 1, low (islands more than 1,000 km east of the Andesite line); 2, moderate (islands east of the Andesite line but within 1,000 km of it); 3, high (islands west of the Andesite line).

Asian dust fallout values were taken or interpolated from refs 16 and 17 plus comments by J. Prospero.

Statistical analyses

Bivariate Spearman correlation coefficients, associated probability values (*P*) and the corresponding bivariate regression coefficients were calculated between the two outcome variables and nine independent variables.

Multivariate regression of each outcome variable on the independent variables employed robust linear regression methods[12] that minimized the absolute unsigned difference (not the squared difference) between observed and model-predicted values to yield least absolute deviation estimates of regression coefficients. We employed this method because the outcome variables are scored on a five-point scale and do not follow a gaussian distribution. Conventional multiple regression that instead minimizes the squared difference is in principle best for continuous measures and gaussian distributions; however, in practice robust and conventional multiple regression yielded virtually identical final models for our data sets (Supplementary Table S7). Initially, all independent variables were included in the model, and then variables with $P > 0.15$ were eliminated iteratively by backwards stepdown robust regression. Variables retained in the final models had $P \leq 0.05$, or $P < 0.0001$ in half of the cases. Log transforms were made on *A*, *D*, elevation and rainfall to obtain distributions more symmetrical and much closer to gaussian. These transformations also created a more linear relation to the outcomes.

Whereas multivariate regression assumes effects of independent variables to be linear, additive and non-interacting, the classification tree method does not make those assumptions and thus lends itself to detecting possible interactions[13]. Recursive binary partitioning is used to predict outcome scores by creating a tree consisting of groups of data points with outcome scores as different as possible between groups, and as similar as possible within groups. Each value of each independent variable is used to split the data into two groups provisionally, and that independent variable value is selected that creates the largest between-group difference relative to within-group variability. The process is repeated, splitting each such group into two further groups, until the final groups are 'pure' (all outcome values identical), sample sizes within a group are too small (less than five), and/or the mean difference between groups is not significant at the $P < 0.1$ level. In practice, all of our groups differed at least at $P < 0.03$, and usually at $P < 0.0001$. Variables entering the tree at earlier (higher) steps are more important than those entering at later (lower) steps.

Before reporting 'final' multiple regression and tree models for each data set (full or reduced) with or without *A* as an independent variable, we calculated model-predicted values of the two outcome variables at each data point, and computed and examined each residual value (predicted value minus actual value). Histograms and normal probability plots of these residual values showed that these errors had a bivariate symmetric unimodal distribution, demonstrating that the robust parametric approach was reasonable despite our semiquantitative deforestation and replacement scales.

For further details see Supplementary Methods.

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Male mammals respond to a risk of sperm competition conveyed by odours of conspecific males

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Sperm competition occurs when a female copulates with two or more males and the sperm of those males compete within the female's reproductive tract to fertilize her eggs[1,2]. The frequent occurrence of sperm competition has forced males of many species to develop different strategies to overcome the sperm of competing males[1,3]. A prevalent strategy is for males to increase their sperm investment (total number of sperm allocated by a male to a particular female) after detecting a risk of sperm competition[1,3,4]. It has been shown that the proportion of sperm that one male contributes to the sperm pool of a female is correlated with the proportion of offspring sired by that male[5,6]. Therefore, by increasing his sperm investment a male may bias a potential sperm competition in his favour[5,7,8]. Here we show that male meadow voles, *Microtus pennsylvanicus*, increase their sperm investment when they mate in the presence of another male's odours. Such an increase in sperm investment does not occur by augmenting the frequency of ejaculations, but by increasing the amount of sperm in a similar number of ejaculations.

Increases in sperm investment in response to a risk of sperm competition have been reported in many groups of animals, such as insects[9,10], fish[11] and birds[12]. In mammals, similar reports are only indirect, in that risk of sperm competition was cued by the fact that males had not guarded the female before copulatory behaviour[13,14]. Although mate guarding is an evolutionary response to minimize the risk of sperm competition, males ultimately assess particular risks of sperm competition in relation to other conspecific males[5]. Males may directly determine if another male has recently copulated with a particular female, for example, by detecting the presence of semen in her reproductive tract[15]. Often, however, a male may not know whether a female has copulated previously or whether a female will copulate with other males after he abandons her. In such cases, the most obvious way for a male to assess the risk of sperm