Rapid ecosystem recovery from diffuse pollution after the Great Irish Famine

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Abstract

Remarkably little is known about the effectiveness or rates of recovery of aquatic ecosystems from reductions in human-associated pressures at landscape scales. The retention of anthropogenic contaminants within ecosystems can retard rates of recovery considerably, while the trajectories of recovery processes vary with the extent of anthropogenic disturbance and the resilience of biotic assemblages. The Great Irish Famine of 1845-1850 comprised one of the most significant human disasters of the nineteenth century, causing the death of approximately one million people and the emigration of a further two million from the country between 1845 and 1855. We found, through analysis of detailed historical census data combined with paleolimnological investigation of sedimentary nutrient concentrations, stable isotope ratios and diatom assemblages, that the trophic level of Lough Carra, a largely shallow calcareous lake in the west of Ireland with no urban areas or point sources of any significance, reduced considerably during and immediately after the Great Famine, shifting to new equilibria within just 2 to 10 years. Our results demonstrate that the reduction of human pressures from diffuse sources at landscape scales can result in the rapid and monotonic recovery of aquatic ecosystems. Moreover, the recovery of ecosystems from diffuse pollution need not necessarily take longer than from pollution from point sources.

Keywords: disturbance, resilience, point source, nutrients, landscape, depopulation, eutrophication

Introduction

As the extent and intensity of human influence on the biosphere continue to increase, there is a critical need to manage ecosystems in ways that maximize their integrity. Inherent in this is the ability to predict rates and trajectories of recovery after disturbance (Peterson et al. 2003, Lotze et al. 2006). Remarkably little is known, however, about the effectiveness or rates of ecosystem recovery from rapid and large-scale human depopulation and the consequent reduction in their associated pressures. Anthropogenic contaminants can be retained within ecosystems for long periods (Withers et al. 2001, Kretzschmar and Schäfer 2005, Banks et al. 2006) and can, thus, retard rates of recovery considerably (Peterson et al. 2003, Schippers et al. 2006). Consequently, historic land use can have persistent effects for centuries (Knops and Tilman 2000, Fraterrigo et al. 2005, McLauchlan et al. 2007, Matamala et al. 2008). Further, in some cases, full recovery may never occur owing, for example, to hysteretic shifts in ecosystem structure, loss of native species pools and genotypic diversity, shifts in species dominance and trophic structure or changes in landscape connectivity and organization (Rietkerk et al. 2004, Suding et al. 2004, Reusch et al. 2005, Lotze et al. 2006). Moreover, both rates and trajectories of recovery can differ significantly from those of impact processes (Hjermann et al. 2004, Zhao et al. 2005, Ibelings et al. 2007) which makes our ability to predict the nature and rates of recovery at ecosystem scales remarkably poor.

Eutrophication from nutrient enrichment comprises a globally important anthropogenic pressure on aquatic ecosystems (Smith et al. 2006, Smith and Schindler 2009). Increased transfer of phosphorus to water is considered as the primary cause of eutrophication of freshwaters, particularly in northern temperate lakes (Schindler 1978).

Lake restoration efforts based on reducing external loading of phosphorus have, however, met with varied levels of success and can be affected significantly by, for example, the relative importance of internal nutrient loading (Marsden 1989, Sas 1989, Søndergaard et al. 2003, Jeppesen et al. 2005), historical loading history (Jeppesen et al. 1991), lake retention time (Kilinc and Moss 2002, Søndergaard et al. 2005) and fish community structure (Jeppesen et al. 1990, Hansson et al. 1998). The length of time required to achieve discernable decreases in lake water column total phosphorus concentrations after reduction in point source nutrient loading has been shown to vary commonly from 10 to 15 years (Jeppesen et al. 2005). Some lakes have, however, shown no signs of recovery even 20 years after reduction of phosphorus input (Jeppesen et al. 2005, Moss et al. 2005).

The great majority of, if not all, efforts to restore lakes through the reduction of external nutrient loading have been based primarily upon diversion, removal or improved treatment of point sources of nutrients (see, for example, Marsden 1989, Sas 1989, Jeppesen et al. 2005). Owing, however, to the considerable difficulties involved with the effective manipulation and management of whole catchments, little is known about rates of lake recovery from catchment-scale reductions in anthropogenic disturbance. Rates of lake recovery from diffuse pollution may be lengthened considerably compared with that from point sources due to the retention of nutrients and other substances within soil matrices (*e.g.* Johnston and Poulton 1992, Withers et al. 2001, Kretzschmar and Schäfer 2005, Banks et al. 2006, Bunemann et al. 2006). Lag times of the order of years to decades might, therefore, be expected to occur between initial reductions of agricultural intensity and consequent decreases in rates of diffuse nutrient transfer to drainage networks (Schippers et al. 2006).

The Great Irish Famine of 1845-1850 comprised one of the most significant human disasters of the nineteenth century, causing the death of approximately one million people and the emigration of a further two million from the country between 1845 and 1855 (Póirtéir 1995). This altered permanently the demographic, political and cultural landscape not only of Ireland, but also, in particular, of the United States and Great Britain. The famine resulted in the dramatic depopulation of the Irish landscape, particularly in western regions where reductions of over 40% of the human population were recorded between 1841 and 1851. As lakes act as sinks for materials from their catchments, paleolimnology comprises one of the few techniques supporting quantification of rates of ecosystem-scale change over discrete intervals of time (Carpenter 2003, Smol 2008) and has, therefore, the potential to provide holistic insight into rates and trajectories of ecosystem recovery after the Great Famine. To this end, we took two sediment cores from the two deepest and most geochemically distinct basins (Hobbs et al. 2005) of Lough Carra, a mostly shallow (mean depth 1.8 m; max depth 19 m) calcareous lake (surface area 15.6 km^2) located in a low-lying (mean elevation 30 m ASL) agricultural landscape in the west of Ireland (Fig. 1). The catchment of Lough Carra (area 114 km^2) has never contained urban areas or contaminant point sources of any significance and, thus, provides an excellent location for the examination of rates of ecosystem recovery from human depopulation and associated reductions in diffuse nutrient pollution at the landscape scale. After establishing radiometric chronologies for the cores, we quantified the structure of historic diatom assemblages, ratios of the stable isotopes $\delta^{13}C$ (for organic material only) and $\delta^{15}N$ and the concentrations and accumulation rates of particulate organic matter and key nutrients. Further, using historic census data with high spatial and temporal resolutions, we were also able to estimate human and livestock population densities for the Carra catchment and use those data to estimate changes in the primary sources of nutrients to the lake from the period immediately subsequent to the Great Famine through to the present day.

Material and methods

Core sampling and analyses

Sediment cores were taken from the deepest points in the northern (53.731° N, 09.263° W) and middle (53.714° N, 09.253° W) basins of Lough Carra (Fig. 1) in July 2002 using a Lincoln piston corer of 5 cm diameter. Core sediments were extruded into 1 cm segments immediately after collection, placed in polygrip plastic bags and stored in darkness at 4ºC. Quantification of total phosphorus (TP) followed Eisenreich *et al.* (1975) after nitric acid digestion in a CEM® MDS-2000 microwave (CEM Corporation, North Carolina, USA). Percent organic matter was determined by loss-on-ignition of approximately 2 g of dry sediment at 550˚C for 3 hours (Heiri et al. 2001). Organic carbon and nitrogen were quantified by flash combustion at 900ºC in a Carlo Erba® 1112 Series Elemental Analyzer (Thermo Scientific Inc., Massachusetts, USA) after removal of inorganic carbon with sulfurous acid. Ratios of the stable isotopes $\delta^{15}N$ and $\delta^{13}C_{org}$, the latter corrected for historic $\delta^{13}C$ depletion of atmospheric CO_2 (Schelske and Hodell 1995), were quantified with a Thermo® Deltaplus continuous flow isotope ratio mass spectrometer (Thermo Scientific Inc., Massachusetts, USA) and are reported relative to, respectively, air and Vienna Pee Dee Belemnite.

Radiometric dating

After grinding to less than approximately 1 mm particle size, the concentrations of gamma-emitting ^{210}Pb, ^{214}Pb, ^{214}Bi, ^{137}Cs and ^{241}Am were determined by placing dried sediments in a calibrated geometry and counting in a high-resolution, low-background, p-type germanium well detector. Energy and efficiency calibration was done using a mixed radionuclide standard supplied by Cerca Framatome ANP (Pierrelatte, France; code: 7081/4) and a separate ^{210}Pb standard supplied by Amersham International (Amersham, UK; code: S6/19/110). ^{210}Pb$_{\text{excess}}$ (excess or unsupported ^{210}Pb) activity was calculated from the total ^{210}Pb activity by subtracting the terrestrial (supported) ^{210}Pb component, which was calculated as the mean activity of ^{214}Pb and ^{214}Bi for the sample. Chronologies and sediment accumulation rates were estimated using the constant rate of supply (CRS) model (Appleby and Oldfield 1978). Modeled CRS chronologies were validated using dates determined independently from the well-known pattern of nuclear fallout input from anthropogenic ^{137}Cs and ^{241}Am. The mean sediment accumulation rate quantified directly for the CRS-dated portion of the core was used to estimate chronologies for the lower regions of the core where ^{210}Pb$_{\text{excess}}$ activity was not detectable. The core from the northern basin was dated radiometrically with chronological control extended to the middle basin core by correlation of down-core variation in sediment properties. Chemical accumulation rates, expressed as g m^{-2} a^{-1}, were calculated as the product of chemical concentrations and dry mass accumulation rates.

Census data and modeling of historic TP loads

Data on historical human population densities were obtained from the Central Statistics Office of Ireland for the period 1841-2002, with a mean (± s.d.) of 8 ± 4.2 years between each census (range = 2-20 years). Human population data were available for the entire period at the level of the District Electoral Division (DED), which is the finest census resolution possible. The Carra catchment encompasses 10 DEDs, each with a mean (± s.d.) area of 28.1 ± 9.3 km^2. Historical land cover, livestock density and farm holding data were obtained for the period 1851-2002, with a mean (± s.d.) of 8.3 ± 3.1 years between each census (range = 3-15 years). These data were, however, available at DED level only for 1851 and from 1937-2000 and were recorded at the level of the Rural District (RD) between 1861 and 1933. The Lough Carra catchment is located within two RDs; Castlebar (588 km^2; 14% in catchment) and Ballinrobe (570 km^2; 6% in catchment). Calculations of human and livestock densities, land cover and farm holdings in the catchment were estimated by weighted averaging based on the proportion of DEDs and, where necessary, RDs located within the catchment. This method thus assumed a homogenous distribution of people, livestock and land use within DEDs and RDs.

Historic TP loads from the catchment of Lough Carra to the lake were estimated using the export coefficient model of Johnes *et al*. (1996) for calcareous catchments. The application of this model to the Carra catchment works extremely well and has been validated with actual measurements of nutrient loading from the catchment in addition to measurements of in-lake nutrient concentrations (Donohue, unpublished data). Due, however, to high variation in the spatial resolution, and hence representativeness, of the agricultural census data, the model was used only to elucidate temporal patterns in the proportional contribution of key nutrient sources over the period examined.

Diatom analyses

Diatom remains were quantified from, respectively, 10 and 11 samples located throughout the north and middle basin cores within which high quality of valve preservation was found. Diatom slides were prepared following Battarbee *et al*. (2001), with 300-500 valves counted per slide, all of which were identified to species level following Krammer and Lange-Bertalot (1986-1991). Variation in the structure of diatom assemblages in these samples among the three main phases of lake productivity indicated by the biogeochemical data from the cores (*i.e.* pre-famine; 1870-1960 and post-1960; see Results) was examined with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001). Lake basin (random factor) and productivity phase (fixed factor) were independent variables in this mixed-effects model, which was based on a Bray-Curtis (Bray and Curtis 1957) similarity matrix calculated from log(x+1)-transformed proportional abundance data and was done with 9999 permutations under the reduced model as recommended by Anderson (2006) using PRIMER® Version 6.1.

The composition of diatom assemblages from the north basin core was used to infer historic water column TP concentrations in Lough Carra using European Diatom Database (EDD) software for palaeoenvironmental reconstructions (Juggins 2001). Match analogue technique (Birks et al. 1990, Jones and Juggins 1995) was used to identify datasets with the closest matches to the fossil samples. Historic diatom-inferred water column TP (DI-TP) concentrations were estimated using locally-weighted weighted averaging (Birks et al. 1990) with inverse de-shrinking because reconstructed values lay closer to the mean of the training set values (Juggins 2001). Analysis of variance (ANOVA) was then used to examine whether temporal patterns in modeled DI-TP concentrations concurred with those of the biogeochemical data from the cores by examining whether they varied among the three lake productivity phases described previously. No attempt was made to model DI-TP concentrations from the mid basin core as in excess of 25% of diatom taxa from the core were absent from the EDD (Birks 1998).

Results

$^{210}Pb_{excess}$ activity concentrations declined exponentially with depth in the North Basin core (Fig. 2), consistent with a relatively constant rate of sediment accumulation. Application of the constant rate of supply (CRS) radiometric dating model yielded a mean (± s.d.) sediment accumulation rate of 0.156 ± 0.03 g cm^{-2} a^{-1}. The core chronology is supported strongly by the ^{137}Cs profile (Fig. 2), which shows two relatively well-resolved peaks corresponding to radioactive fallout from Chernobyl (1986) and global nuclear weapons fallout (onset: 1954; peak: 1963). The presence of ^{241}Am in the layers corresponding to the deeper peak in ^{137}Cs confirm its origin as weapons fallout.

Chronologies for the highly consistent profiles from the two sediment cores show a dramatic and monotonic decline in both sedimentary δ^{15}N and organic matter in the period immediately following the Great Famine of 1845-1850 (Fig. 3). Considerable depletions in δ^{15}N of the order of, respectively, 1.25 and 1.13‰ in the northern and middle basin cores were found over a two year period immediately after the famine while the concurrent monotonic reduction in sedimentary organic matter content took place over approximately ten years. These decreases were coincident with a 39.8% reduction in the human population recorded between 1841 and 1861 (Fig. 3). These shifts to new equilibria were also contemporaneous with monotonic reductions in concentrations of sedimentary phosphorus (Fig. 4). Although following a similar pattern, phosphorus accumulation rates were considerably more variable during this period, particularly in the core from the northern basin. Molar ratios of C_{org}:N and sedimentary $\delta^{13}C_{org}$ (Fig. 4) were highly consistent (Pearson Product-Moment correlation; $r = 0.906$, $p < 0.0001$, $df = 28$) and generally increased over an approximately 20 year period during and subsequent to the famine. This pattern was, however, punctuated by a distinct peak in both ratios which took place immediately subsequent to the phase of declining sedimentary $\delta^{15}N$ stable isotope ratios and organic matter after the famine. Simultaneous and consistent enrichment of sedimentary $\delta^{15}N$, organic matter content and both concentrations and accumulation rates of phosphorus were found towards the top of both cores, from the latter half of the twentieth century to the present and particularly in the last two decades, concurrent with declining molar organic C_{org}:N ratios (Figs. 3 & 4).

Even though the structure of lake diatom assemblages differed significantly between the two sediment cores, significant differences were also found among the three main phases of lake productivity indicated by the biogeochemistry of the cores (*i.e.* pre-famine; 1870-1960 and post-1960; Table 1(a)). *A posteriori* pairwise tests found that the structure of diatom assemblages during the post-famine (1870-1960) phase differed significantly from those prior to the famine ($t = 2.06$, $p = 0.02$). DI-TP concentrations estimated from the north basin core also varied significantly with lake productivity phase (Table 1(b)) and comprised (mean ± s.d.) 15 ± 2.6 $\mu g\ L^{-1}$ for the period prior to the famine, 12.2 ± 2.4 $\mu g\ L^{-1}$ for 1870-1960 and 19.6 ± 1.8 $\mu g\ L^{-1}$ since 1960. *A posteriori* tests found, however, that DI-TP concentrations differed significantly only between the post-1960 and 1870-1960 productivity phases (least significant difference *post hoc* test; $p = 0.003$).

The relative importance of the primary sources of phosphorus to the lake (Table 2) appear to have changed considerably in the last 150 years, with human effluent comprising the main source up to 1900, whereas cattle have provided the majority of TP loading to the lake since 1970 (Fig. 5(a)). This increase in the relative importance of cattle farming has been concurrent with a consistent increase in the number of larger farms (>20 ha) in the catchment (Fig. 5(b)) owing to the aggregation of small farms and the associated removal of field boundaries.

Discussion

Our results suggest strongly that the trophic level of Lough Carra (*sensu* Rodhe 1969, Wetzel 2001) reduced dramatically over less than 10 years after the rapid and large-scale depopulation of the landscape and reduction of associated human pressures that occurred as a result of the Great Famine. The sedimentary profiles of $\delta^{15}N$ and organic matter from the two sediment cores indicate that considerable and monotonic declines in the transfer of nutrients and particulate organic matter from the catchment and associated reductions in lake productivity took place over approximately, respectively, 2 and 10 years, concurrent with a 40% decline in human population density. The depletion in sedimentary $\delta^{15}N$ during this period likely reflect both reduced input of diffuse N from the catchment and associated decreased utilization of nitrate by algae in the lake (Bunting et al. 2007). Although abandonment of agriculture and the associated tightening of the N-cycle has also been found to reduce $\delta^{15}N$ in upper soil layers (Compton et al. 2007), it is unlikely that decreases of the magnitude observed here could be accounted for by this mechanism over such a short timescale as 2 years. These shifts to new equilibria were also concurrent with reductions in both concentrations and accumulation rates of sedimentary phosphorus, which further support the premise that nutrient losses from the catchment to the lake declined as a result of reductions in human population pressure and associated agricultural intensity. The possibility of post-depositional mobilization of phosphorus upon sediment deposition is considered to be low in Lough Carra owing to the low likelihood of historical changes in redox states in the lake (Hobbs et al. 2005).

The remarkable similarity and consistency between the two cores, which were taken from the two most geochemically distinct basins in the lake (Hobbs et al. 2005), demonstrate that the patterns found here occurred throughout the lake system. C_{org}:N ratios from both cores suggest strongly that the organic matter deposited in Lough Carra comprised significant contributions from both allochthonous (produced in the catchment) and autochthonous (produced in the lake) sources. Profiles of both C_{org}:N and $\delta^{13}C_{org}$ indicate that the relative contributions of these sources has varied considerably over the last 200 years and particularly after the Great Famine. Increasing ratios of both C_{org}:N and $\delta^{13}C_{org}$ during this period indicate reduced contribution of lacustrine productivity to sedimentary organic matter and increased dominance of terrestrial organic matter, for which C_{org}:N ratios vary typically between 20 and 100 (Jasper and Gagosian 1989). This is consistent with reduced nutrient losses from the catchment after the famine resulting in decreased in-lake productivity. These gradual increases in both C_{org}:N and $\delta^{13}C_{org}$ were punctuated by a dramatic peak in both ratios in both cores at the end of the period of decreasing trophic level after the famine which is highly indicative of a pulse of terrestrial organic matter into the lake. Historical records (Board of Public Works 1853) suggest strongly that this pulse is attributable to drainage works that took place in the lake catchment in the summer of 1852 and subsequent extreme flooding, the worst in living memory at the time, that obliterated those works later that winter, two years after the famine. The estimated CRS date for this event, however, which was estimated indirectly using the mean sedimentation rate from the upper portion of the core, is 1866. After extensive searches, however, we could find nothing else either in the literature or from local knowledge that may have accounted for this event. On balance, therefore, our results would suggest that the accumulation rate of sediment in the lower portion of the core where the chronology was estimated indirectly was slightly higher than that estimated for the upper region of the core and that the observed reduction of trophic level of Lough Carra took place during, rather than immediately subsequent to, the Great Famine of 1845-1850.

Sources of phosphorus to the lake appear to have changed dramatically since the famine, driven initially directly by reductions in human populations in the catchment. The majority of recent inputs of phosphorus to the lake was, however, derived directly from intensification of catchment use associated with cattle farming, and demonstrates a dramatic change in catchment land use and sources of nutrients over the last 150 years. Further, the size of farms has also increased considerably, in particular since the 1950s. These factors, coupled with the associated removal of field boundaries, suggest that the process of recovery from current anthropogenic pressures would likely differ from, and could be more difficult and lengthy than, that which occurred as a result of the Great Famine. Further, there is evidence that the surface lakebed sediments in Lough Carra have approached their maximum sorption capacity for phosphorus (Hobbs et al. 2005). Beyond this point, there is a strong possibility that the lake could switch rapidly from its current state of relatively clear water with extensive macrophyte growth to an alternative stable state with a highly turbid water column (Scheffer et al. 2001). Recovery from the latter state would be expected to take considerably longer than required after the Great Famine and would necessitate much management effort, potentially incurring substantial financial cost.

Results from our biogeochemical indicators of historical catchment conditions and inferred shifts in ecosystem equilibria are supported strongly by the fact that diatom assemblages varied significantly among the three phases of lake productivity indicated by the cores. Further, diatom-inferred TP concentrations also varied significantly among the lake productivity phases and were lowest in the period subsequent to the famine. Results from the analyses of diatom assemblages in the cores therefore support the assertion that biological change occurred in the lake coincident with the biogeochemical shifts to new equilibria that occurred after the Great Famine. Even though this study suffers from the constraints associated normally with uncontrolled observational studies, the fact that such consistent results were obtained from the analysis of a number of independent proxies provides strong support for our conclusions.

The fact that Lough Carra is largely shallow with, therefore, a relatively important contribution of benthic processes to lake ecology, would have been expected to retard recovery of the lake significantly (Moss et al. 1996). The rapid establishment of new ecosystem equilibria within two to ten years following the Great Famine is, however, comparable with the most expeditious response of lakes whose nutrient loading from point sources have been reduced using modern engineering solutions (Jeppesen et al. 2005). This is in spite of the fact that nutrients and other substances can be retained by soil matrices for long periods, potentially delaying recovery from landscape-scale anthropogenic disturbance significantly (Schippers et al. 2006). The legacy of historic anthropogenic disturbance can potentially last for centuries, even after rapid human depopulation has taken place (Webb and Newman 1982, Paul 1991, Knapp 1992, Brown 2000). Our results demonstrate, however, that the swift reduction of human-associated pressures from diffuse sources at landscape scales can, in some circumstances, result in the rapid and monotonic recovery of lake ecosystems. Recovery of ecosystems from diffuse pollution need not necessarily, therefore, take longer than from pollution from point sources.

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Literature cited

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32-46.

Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62:245-253.

Appleby, P. G. and F. Oldfield. 1978. The calculation of lead-210 dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. Catena 5:1-8.

Banks, M. K., A. P. Schwab, and C. Henderson. 2006. Leaching and reduction of chromium in soil as affected by soil organic content and plants. Chemosphere 62:255-264.

Battarbee, R. W., V. J. Jones, R. J. Flower, N. G. Cameron, H. B. Bennion, L. Carvalho, and S. Juggins. 2001. Diatoms. Pages 155-202 *in* J. P. Smol, H. J. B. Birks, and W. M. Last, editors. Tracking Environmental Change Using Lake Sediments, Volume 3: Terrestrial, Algal and Siliceous Indicators. Kluwer Academic Publishers, Dordrecht.

Birks, H. J. B. 1998. Numerical tools in paleolimnology: progress, potentialities and problems. Journal of Paleolimnology 20:307-332.

Birks, H. J. B., J. M. Line, S. Juggins, A. C. Stevenson, and C. J. F. Ter Braak. 1990. Diatoms and pH reconstruction. Philosophical Transactions of the Royal Society of London Series B - Biological Sciences 327:263-278.

Board_of_Public_Works. 1853. 21st Annual Report. Alexander Thom & Sons, Dublin, Ireland.

Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325-349.

Brown, K. 2000. Ecosystem recovery: Ghost towns tell tales of ecological boom and bust. Science 290:35-37.

Bunemann, E. K., D. P. Heenan, P. Marschner, and A. M. McNeill. 2006. Long-term effects of crop rotation, stubble management and tillage on soil phosphorus dynamics. Australian Journal of Soil Research 44:611-618.

Bunting, L., P. R. Leavitt, C. E. Gibson, E. J. McGee, and V. A. Hall. 2007. Degradation of water quality in Lough Neagh, Northern Ireland, by diffuse nitrogen flux from a phosphorus-rich catchment. Limnology and Oceanography 52:354-369.

Carpenter, S. R. 2003. Regime Shifts in Lake Ecosystems: Pattern and Variation. Ecology Institute, Oldendorf/Luhe, Germany.

Compton, J. E., T. D. Hooker, and S. S. Perakis. 2007. Ecosystem N distribution and delta N-15 during a century of forest regrowth after agricultural abandonment. Ecosystems 10:1197-1208.

Eisenreich, S. J., R. T. Bannerman, and D. E. Armstrong. 1975. A simplified phosphorus technique. Environmental Letters 9:43-53.

Fraterrigo, J. M., M. G. Turner, S. M. Pearson, and P. Dixon. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. Ecological Monographs 75:215-230.

Hansson, L. A., H. Annadotter, E. Bergman, S. F. Hamrin, E. Jeppesen, T. Kairesalo, E. Luokkanen, P. A. Nilsson, M. Søndergaard, and J. Strand. 1998. Biomanipulation as an application of food-chain theory: Constraints, synthesis, and recommendations for temperate lakes. Ecosystems 1:558-574.

Heiri, O., A. F. Lotter, and G. Lemcke. 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25:101-110.

Hjermann, D. O., G. Ottersen, and N. C. Stenseth. 2004. Competition among fishermen and fish causes the collapse of Barents Sea capelin. Proceedings of the National Academy of Sciences of the United States of America 101:11679-11684.

Hobbs, W., K. Irvine, and I. Donohue. 2005. Using sediments to assess the resistance of a calcareous lake to diffuse nutrient loading. Archiv für Hydrobiologie 164:109-125.

Ibelings, B. W., R. Portielje, E. Lammens, R. Noordhuis, M. S. van den Berg, W. Joosse, and M. L. Meijer. 2007. Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. Ecosystems 10:4-16.

Jasper, J. P. and R. B. Gagosian. 1989. Glacial-intergacial climatically forced $\delta^{13}C$ variations in sedimentary organic matter. Nature 342:60-62.

Jeppesen, E., J. P. Jensen, P. Kristensen, M. Sondergaard, E. Mortensen, O. Sortkjaer, and K. Olrik. 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. Hydrobiologia 200:219-227.

Jeppesen, E., P. Kristensen, J. P. Jensen, M. Søndergaard, E. Mortensen, and T. Lauridsen. 1991. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. Memorie dell'Instituto Italiano di Idrobiologia 48:127-148.

Jeppesen, E., M. Sondergaard, J. P. Jensen, K. E. Havens, O. Anneville, L. Carvalho, M. F. Coveney, R. Deneke, M. T. Dokulil, B. Foy, D. Gerdeaux, S. E. Hampton, S. Hilt, K. Kangur, J. Kohler, E. Lammens, T. L. Lauridsen, M. Manca, M. R. Miracle, B. Moss, P. Noges, G. Persson, G. Phillips, R. Portielje, C. L. Schelske, D. Straile, I. Tatrai, E. Willen, and M. Winder. 2005. Lake responses to reduced nutrient loading - an analysis of contemporary long-term data from 35 case studies. Freshwater Biology 50:1747-1771.

Johnes, P., B. Moss, and G. Phillips. 1996. The determination of total nitrogen and total phosphorus concentrations in freshwaters from land use, stock headage and population data: Testing of a model for use in conservation and water quality management. Freshwater Biology 36:451-473.

Johnston, A. E. and P. R. Poulton. 1992. The role of phosphorus in crop production and soil fertility: 150 years of field experiment. Pages 45-64 *in* J. J. Scultz, editor.

Phosphatic fertilizers and the environment International Fertilizer Development Centre Muscle Shoals, U.S.A.

Jones, V. J. and S. Juggins. 1995. The construction of a diatom-based chlorophyll *a* transfer function and its application at three lakes on Signy Island (maritime Arctic) subject to differing degrees of nutrient enrichment. Freshwater Biology 34:433-445.

Juggins, S. 2001. The European diatom database. User Guide Version 1.0. Department of Geography, University of Newcastle.

Kilinc, S. and B. Moss. 2002. Whitemere, a lake that defies some conventions about nutrients. Freshwater Biology 47:207-218.

Knapp, P. A. 1992. Secondary plant succession and vegetation recovery in two western Great Basin Desert ghost towns. Biological Conservation 60:81-89.

Knops, J. M. H. and D. Tilman. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. Ecology 81:88-98.

Krammer, K. and H. Lange-Bertalot. 1986-1991. Bacillariophyceae, Parts 1-4. Page 2485 *in* H. Ettl, J. Gerlof, H. Heynig, and D. Mollenhauer, editors. Süßwasserflora von Mitteleuropa, Volume 2. Gustav Fischer Verlag, Stuttgart.

Kretzschmar, R. and T. Schäfer. 2005. Metal retention and transport on colloidal particles in the environment. Elements 1:205-210.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806-1809.

Marsden, M. W. 1989. Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. Freshwater Biology 21:139-162.

Matamala, R., J. D. Jastrow, R. M. Miller, and C. T. Garten. 2008. Temporal changes in C and N stocks of restored prairie: Implications for C sequestration strategies. Ecological Applications 18:1470-1488.

McArdle, B. H. and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290-297.

McLauchlan, K. K., J. M. Craine, W. W. Oswald, P. R. Leavitt, and G. E. Likens. 2007. Changes in nitrogen cycling during the past century in a northern hardwood forest. Proceedings of the National Academy of Sciences of the United States of America 104:7466-7470.

Moss, B., T. Barker, D. Stephen, A. E. Williams, D. J. Balayla, M. Beklioglu, and L. Carvalho. 2005. Consequences of reduced nutrient loading on a lake system in a lowland catchment: deviations from the norm? Freshwater Biology 50:1687-1705.

Moss, B., J. Madgwick, and G. Phillips. 1996. A Guide to the Restoration of Nutrient-Enriched Shallow Lakes. Environment Agency, Broads Authority and European Union Life Programme, Norwich, U.K.

Paul, A. K. 1991. Long-term soil and vegetation recovery in five semiarid Montana ghost towns. The Professional Geographer 43:486-499.

Peterson, C. H., S. D. Rice, J. W. Short, D. Esler, J. L. Bodkin, B. E. Ballachey, and D. B. Irons. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. Science 302:2082-2086.

Póirtéir, C., editor. 1995. The Great Irish Famine. Mercier Press, Cork & Dublin, Ireland.

Reusch, T. B. H., A. Ehlers, A. Hammerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proceedings of the National Academy of Sciences of the United States of America 102:2826-2831.

Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science 305:1926-1929.

Rodhe, W. 1969. Crystallization of eutrophication concepts in Northern Europe. Pages 50-64 Eutrophication: Causes, Consequences, Correctives. National Academy of Sciences, Washington, D.C., U.S.A.

Sas, H., editor. 1989. Lake restoration by reduction of nutrient loading. Expectation, experiences, extrapolation. Academia Verlag Richardz GmbH., St. Augustin.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591-596.

Schelske, C. L. and D. A. Hodell. 1995. Using carbon isotopes of bulk sedimentary organic matter to reconstruct the history of nutrient loading and eutrophication in Lake Erie. Limnology and Oceanography 40:918-929.

Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnology and Oceanography 23:478-486.

Schippers, P., H. van de Weerd, J. de Klein, B. de Jong, and M. Scheffer. 2006. Impacts of agricultural phosphorus use in catchments on shallow lake water quality: About buffers, time delays and equilibria. Science of the Total Environment 369:280-294.

Smith, V. H., S. B. Joye, and R. W. Howarth. 2006. Eutrophication of freshwater and marine ecosystems. Limnology and Oceanography 51:351-355.

Smith, V. H. and D. W. Schindler. 2009. Eutrophication science: where do we go from here? . Trends in Ecology & Evolution 24:201-207.

Smol, J. P. 2008. Pollution of lakes and rivers: a paleoenvironmental perspective. Second edition. Blackwell Publishing, Malden MA.

Søndergaard, M., J. P. Jensen, and E. Jeppesen. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506:135-145.

Søndergaard, M., J. P. Jensen, and E. Jeppesen. 2005. Seasonal response of nutrients to reduced phosphorus loading in 12 Danish lakes. Freshwater Biology 50:1605-1615.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution 19:46-53.

Webb, R. H. and E. B. Newman. 1982. Recovery of soil and vegetation in ghost towns in the Mojave Desert, southwestern United States. Environmental Conservation 9:245-248.

Wetzel, R. G. 2001. Limnology: lake and river ecosystems. Third edition. Academic Press, London.

Withers, P. J. A., A. C. Edwards, and R. H. Foy. 2001. Phosphorus cycling in UK agriculture and implications for phosphorus loss from soil. Soil Use and Management 17:139-149.

Zhao, W. Z., H. L. Xiao, Z. M. Liu, and J. Li. 2005. Soil degradation and restoration as affected by land use change in the semiarid Bashang area, northern China. Catena 59:173-186.

Tables

Table 1. Results of analyses of diatom assemblage structure (a; PERMANOVA) and DI-TP concentrations (b; ANOVA) during the three main phases of lake productivity indicated by the biogeochemistry of core sediments.

	Source of variation	***df***	**Sum of squares**	**Mean square**	***F*-ratio**	***p***
(a)	Lake basin, B	1	5401.4	5401.4	6.8*	≤ 0.0001
	Productivity phase, P	2	4616.9	2308.4	2.6*	0.033
	B*P	2	1776.8	888.4	1.1*	0.33
	Residual	15	11944	796.3		
(b)	Productivity phase	2	83.3	41.7	5.3	0.039
	Residual	7	54.6	7.8		

* Pseudo-*F*-ratio

Table 2. Mean (± s.d.) and range of percentage contributions of the primary sources of phosphorus to the total modelled annual catchment TP loading to Lough Carra for the period 1851-2002 (*n* = 19).

Source	**Mean contribution (%)**	**Range of contribution (%)**
Cattle	33.8 ± 14.3	14.1 – 59.8
Humans	29.1 ± 11.8	15.1 – 52.3
Tillage	13.4 ± 6.9	0.6 – 25.5
Grassland	10.5 ± 5.4	0 – 17
Sheep	9.5 ± 3.3	4.5 – 14.8
Pigs	3.8 ± 1.2	0 – 5.4

Figure legends

Fig. 1. Lough Carra and its catchment, showing the locations of the north (1) and mid (2) basin cores.

Fig. 2. Activity profiles (± s.d.) of $^{210}Pb_{excess}$ (a), ^{137}Cs (b) and ^{241}Am (c) (the latter two profiles with CRS dates) in the north basin core. ^{241}Am was above detection limits in only a limited section of the core.

Fig. 3. Estimated human population density of the Lough Carra catchment, 1841-2002 (a) and profiles (with CRS dates) of sedimentary $\delta^{15}N$ (b) and organic matter (c) in the cores taken from the north (closed squares) and middle (open circles) basins of Lough Carra.

Fig. 4. Profiles (with CRS dates) of concentrations (a) and accumulation rates (b) of total phosphorus and ratios of C_{org}:N (c) and $\delta^{13}C_{org}$ (d) in the cores taken from the north (closed squares) and middle (open circles) basins of Lough Carra

Fig. 5. Historical change in the percentage of modeled total TP load to Lough Carra attributable to humans (closed squares) and cattle (open circles) (a) and the number of farms <20 ha (closed squares) and >20 ha (open circles) in area in the lake catchment (b).

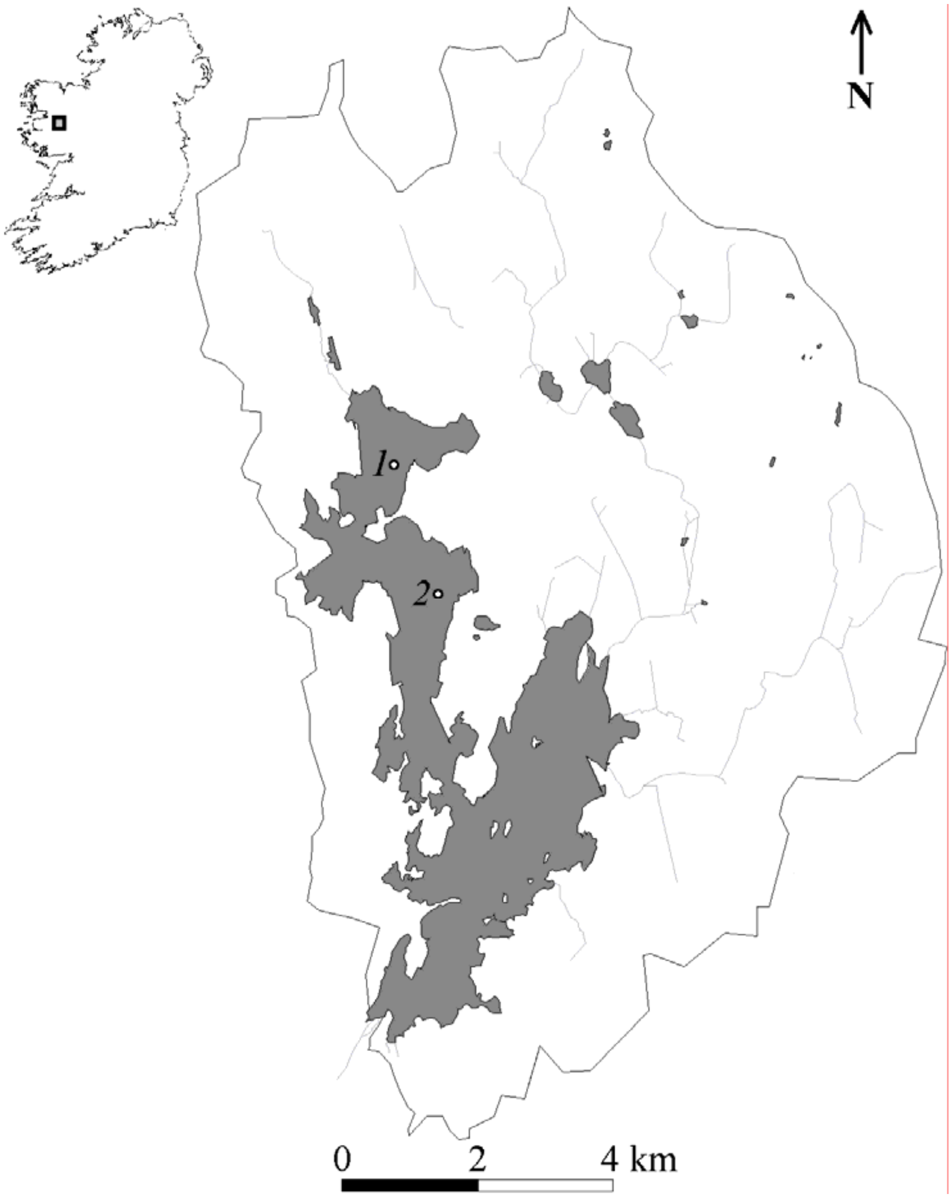
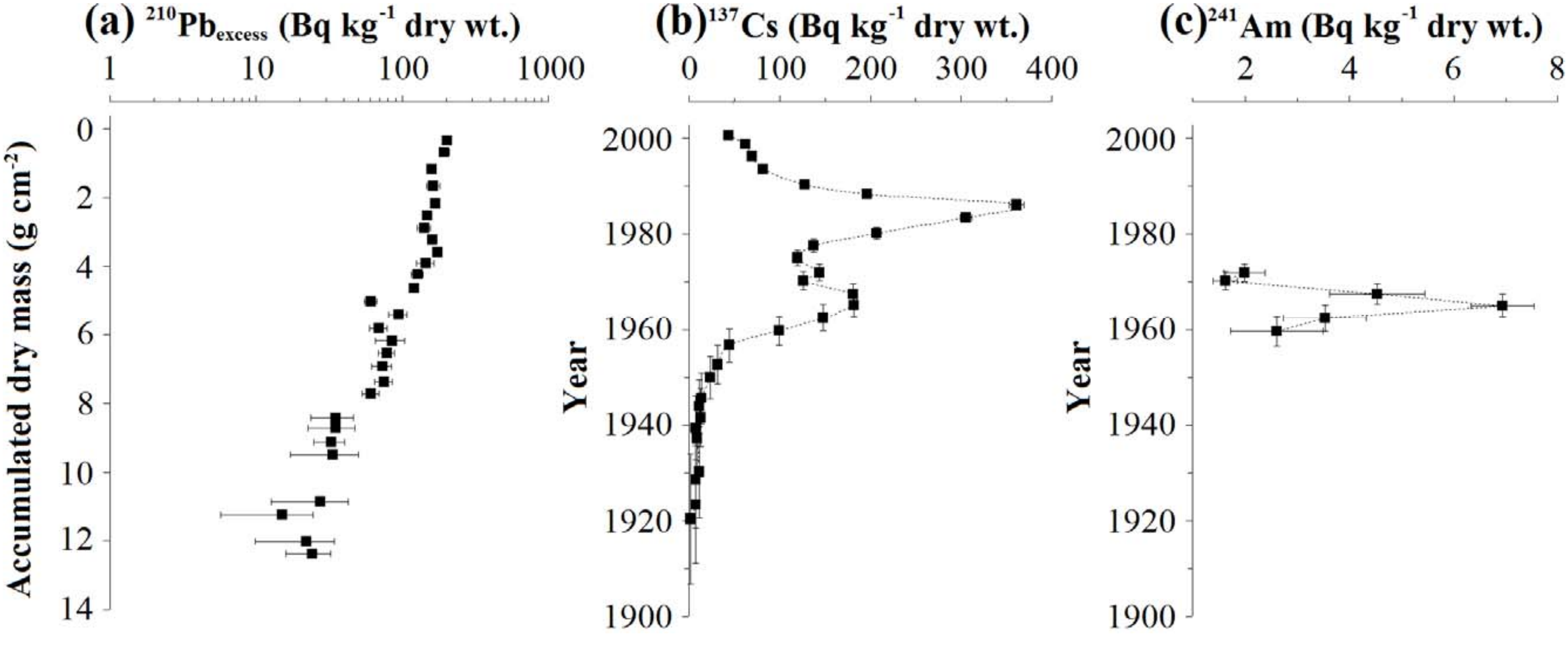


Fig. 1. Donohue *et al.*



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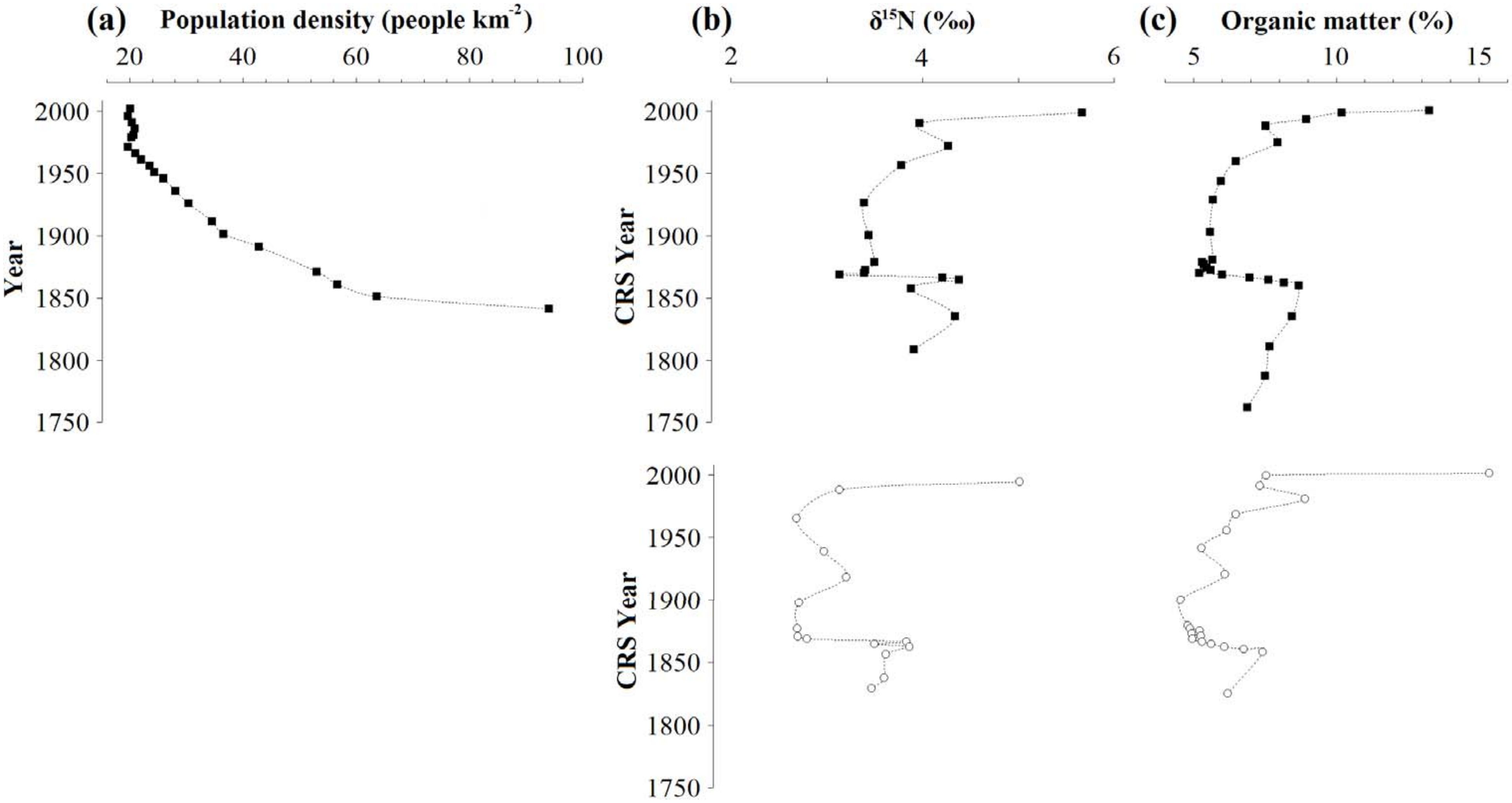

Fig. 3. Donohue *et al.*

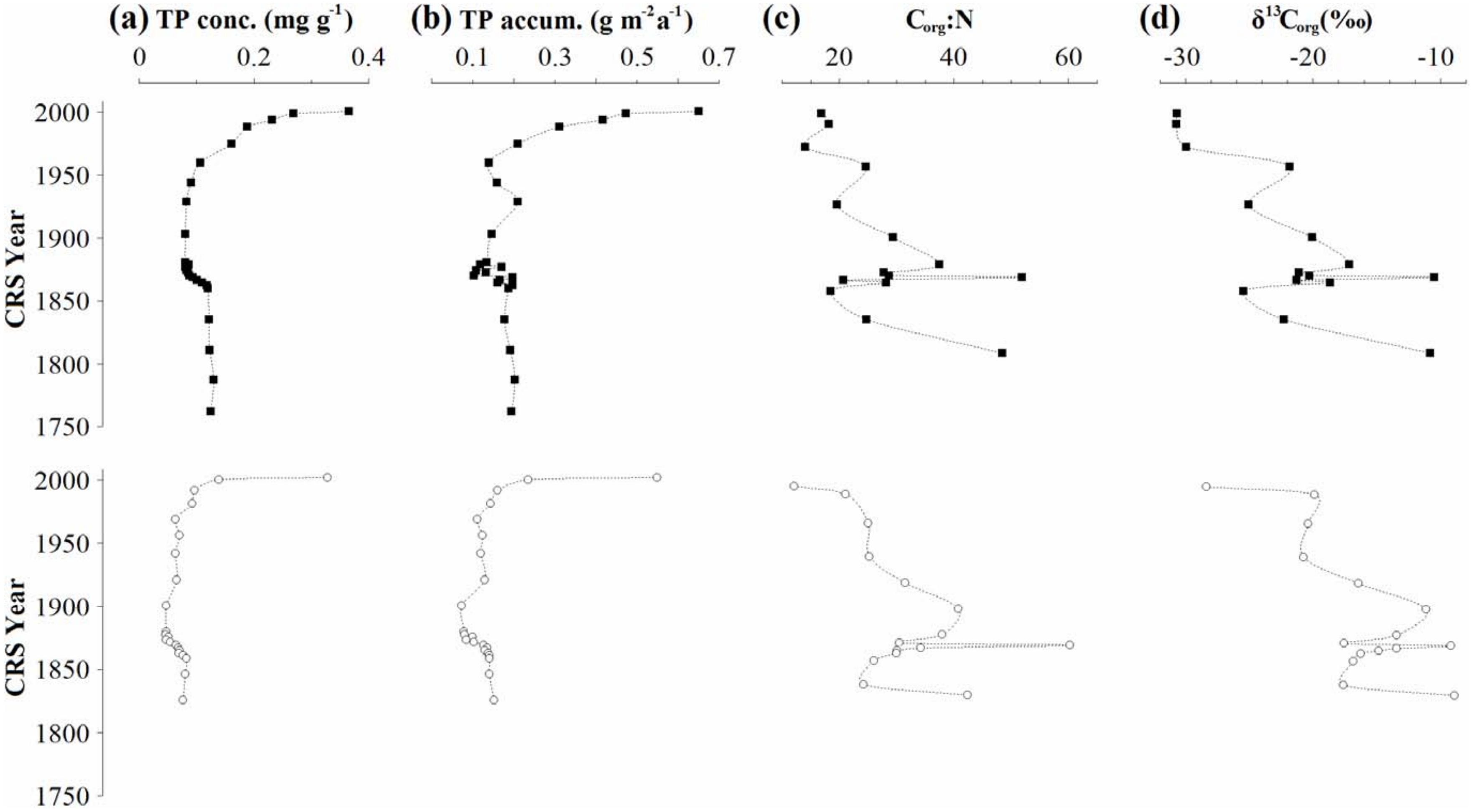

Fig. 4. Donohue *et al.*

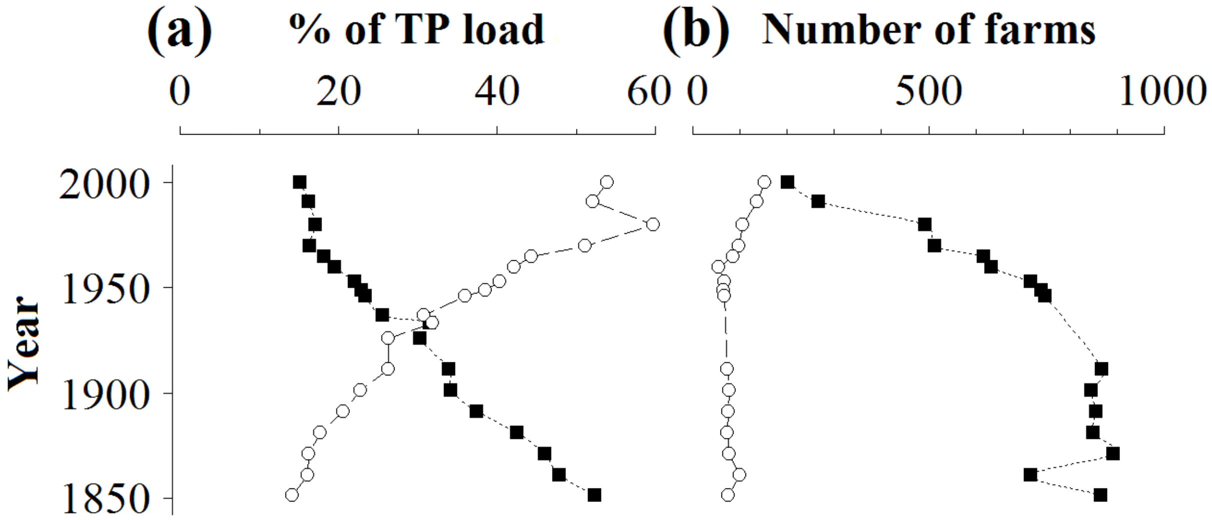

Fig. 5. Donohue *et al.*