

Varying Ecological Successions in Lakes Subdivided by Volcanic Eruption at Akan Caldera, Japan

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Abstract

It is difficult to continuously observe ecological succession processes within lakes occurring over long-time spans. Thus, the process is generally shown as "lake types" or "hydrarch succession" reflected by trophic levels or differing aquatic vegetation, based on inductive inference by comparison of many lakes. Alternatively, long-term changes are simulated via microcosms or mesocosms in experimental systems, or lake history can be reconstructed by sediment analysis. Here, we try to demonstrate lake ecological succession processes over thousands of years by showing an example of lakes with diverse trophic levels and aquatic vegetation which were formed by segmentation inside Akan Caldera in eastern Hokkaido, Japan, due to volcanic eruptions. We found oligotrophic, mesotrophic, eutrophic and dystrophic lake systems in the caldera, despite similar ages and process of origin. Total water phosphorus concentration, defining trophic level, was significantly correlated with the ratio of accumulated watershed area to lake area and volume. Twenty-one species of aquatic macrophytes were classified into five groups clearly corresponding to respective or combinations of trophic level. This study is the first to visualize lake serial stages by documenting a series of trophic levels and associated aquatic vegetation groups as a result of differing eutrophication rates over time.

Introduction

Ecological succession within lakes is not only a major component of freshwater ecology and limnology, but also a platform for diagnosis and management of worldwide deteriorating aquatic environments resulting from human activity since the 20th century¹⁻⁷. In general, lake succession proceeds thusly: when a lake is first formed the water is oligotrophic with a paucity of biota, but the trophic level subsequently increases, as nutrients and minerals inflow from the watershed, and the lake basin shallows from accumulation of sediments. The diversity of biota and biomass increase or fluctuate throughout this process, and eventually the lake attains the state of bog or marsh^{1,2,4,5,8}. Historically, Forel, the "father" of limnology⁵, explained this transition as analogous to human ageing⁹, and this concept has been widely accepted due to both intuitive and experiential evidence^{1,2,5,10}. Lake ecological succession is mostly characterized as "lake succession" or "lake type" based on differences in water quality, including trophic condition, and as "hydrarch succession" according to changes in aquatic flora^{2,6,10,11}. Although the process and rate of succession varies with climatic zones, lake basin size, and initial water quality, in temperate regions lakes and hydrarch succession generally progress as oligotrophic-mesotrophic-eutrophic lake types, and submerged-floating leaved-emergent plants, respectively^{2,4,6,12,13}. However, in any case, as Forel⁹ pointed out when he compared the succession process to human aging, it is impossible to follow a normal lake's evolution, because of the immense time-scales required for a lake to disappear by sedimentation. Therefore, this general picture of long-term succession has been indirectly formed by comparing many lakes with different trophic conditions^{10,12,14-18}, historical reconstruction of sedimentation processes^{6,8,19}, follow-up survey of small-scale dams or reservoirs^{2,20}, and experimental microcosms and mesocosms^{5,21-25}.

Despite these efforts, the perception of ecological succession in large lakes still relies on many assumptions, due to their long durations of biological ageings^{2,21,26,27}. For example, the rate of eutrophication under natural conditions, a leading factor in succession, is thought to vary depending on lake size. However, few studies have successfully demonstrated that lake trophic conditions are related to lake size relative to watershed area^{1,2,4,5}. The main reason for this missing information is how the load of trophic substances and sediments from the watershed is influenced by indigenous variables, such as land form, soil, degree of weathering and erosion, local climate (temperature and rainfall), vegetation, and land use (farmland, factory and urbanization) in addition to the time effect^{1,2,4,5,10}. Accordingly, a set of different size lakes of the same age and with similar watershed environmental conditions is needed to examine if lake trophic condition is related to the lake size and watershed area. In this paper, we offer insight into this problem by comparing a group of lakes in a large caldera. The lakes of Akan Caldera, Hokkaido, Japan, were formed by volcanic eruptions thousands of years ago, which divided a huge caldera lake into several lakes of varying size²⁸⁻³⁰. The watersheds of these lakes share similar

environmental variables, making it possible to test the relationships between trophic conditions and aquatic flora, and lake size relative to watershed area.

Results And Discussion

Study area

Akan Caldera is situated at the southern end of the Akan-Shiretoko Volcanic Chain, a volcanic region in eastern Hokkaido, Japan³⁰. The outer shape of the caldera is oblong (24 km east-west × 13 km north-south)³⁰, and a “central cone”, Mt. O-akan, rises at the center of its inner basin (Fig. 1a, b). Within the caldera there are lakes and marshes of various sizes surrounding Mt. O-akan (Fig. 1a, Supplementary Table S1 online). Lake watersheds are isolated from external input by the caldera-wall^{31,32}, and the water systems, connected by rivers or underground flow^{28,32,33}, are roughly divided north-south and join at the southern foot of Mt. O-akan, where they then discharge through Akan River, the notch in the south caldera-wall (Fig. 1a).

Large lakes are distributed from west to northeast of Mt. O-akan and smaller lakes are localized from south to east (Fig. 1a). This peculiar lake arrangement is a result of the formation history of the caldera and Mt. O-akan. The Akan region has witnessed more than ten large volcanic eruptions in the last 1.5 million years, and the present oblong-shaped caldera was formed by the largest eruption of 200,000 years ago³⁰. After the last large eruption (150,000 years ago), a huge lake, “Ko-akanko” (ancient Lake Akan), was generated in the caldera²⁸⁻³⁰. The lake was narrowed by post-caldera volcanic activity in the southwest part of the caldera, and by 110,000 years ago landform of the inside caldera-wall was almost completed²⁸⁻³⁰. A minor eruption of Mt. O-akan occurred 13,000 years ago slightly southeast of the center of the caldera, and it stopped when the lava flow reached the caldera-wall, so that Ko-akanko was separated into large and small basins²⁸⁻³⁰.

The developmental history of Mt. O-akan also shows that Pond Hyotan and Pond Junsai of the southern water system were first divided from Ko-akanko, and other lakes of the northern water system were formed 5,000 to 2,500 years ago²⁸⁻³⁰. The lake depth charts of the large lakes, Akan, Panke and Penke, show the remains of valleys on the bottom of the inside of the caldera-wall extending as far as the base of Mt. O-akan^{28,31,33}. This suggests that the water level of Ko-akanko was extremely low or the basin was exposed by discharge through the notch before the eruption of Mt. O-akan²⁸. Therefore, the lakes of the northern water system are thought have formed by re-flooding after damming by Mt. O-akan, but the timing of lake formation and the developmental processes are not fully understood.

Akan Caldera occupies a part of Akan-Mashu National Park (designated in 1934³⁴), and is mostly covered with subarctic forests except for a town on the south side of Lake Akan, Akanko-onsen (Fig. 1a, b). Only Lake Akan has been developed as a sightseeing area due to the presence of Marimo, *Aegagropila linnaei*, a ball-shaped green alga designated a Japanese natural treasure^{34,35}. Since the 1950s, the increase in tourism has resulted in eutrophication from sewage discharge. This continued until the 1980s when public sewage treatment service was provided³⁶.

Water quality and lake types

Based on chlorophyll-a (Chl-a) and total phosphorus (TP) levels found in limnological surveys, the ten lakes of Akan Caldera were categorized as oligotrophic (2 lakes), mesotrophic (5 lakes) and eutrophic (3 lakes) (Fig. 2a). Among these lakes, Pond Junsai (eutrophic) had brownish water with high total nitrogen (TN; 0.438 mg l⁻¹), dissolved organic carbon (DOC; 7.1 mg l⁻¹) and Chl-a concentrations (12.5 µg l⁻¹) (Supplementary Table S2 online) and was thus viewed as dystrophic^{6,24}.

Table 1

Combinations indicating strong correlation coefficients (r) between water quality variables and topographic characters (see Supplementary Table S4 online), and occurrence of an outlier. TP: total phosphorus, EC: electrical conductivity, DO: dissolved oxygen, AWA: accumulated watershed area, LA: lake area, LV: lake volume, ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, n.s.: not significant, □: occurrence of an outlier (Lake Akan).

Water quality	Topography			
	Shoreline development	AWA	AWA-LA ratio	AWA-LV ratio
TP	-0.052 ^{n.s.}	0.820 ^{**}	0.665 ^{*□}	0.751 ^{*□}
EC	0.236 ^{n.s.}	0.991 ^{***}	0.720 ^{*□}	0.726 ^{*□}
pH	0.885 ^{***}	0.283 ^{n.s.}	-0.149 ^{n.s.}	-0.205 ^{n.s.}
DO	0.517 ^{n.s.}	-0.395 ^{n.s.}	-0.692 [*]	-0.763 [*]

A correlation matrix was completed on 9 water quality variables and 17 topographic characters (Supplementary Table S4 online). Strong ($|r| \geq 0.7$) and significant ($p < 0.05$, by test of no correlation) correlation coefficients were found between: TP and accumulated watershed area (AWA), TP and AWA-lake volume (LV) ratio (AWA/LV), electrical conductivity (EC) and AWA, EC and AWA-lake area (LA) ratio (AWA/LA), EC and AWA/LV, pH and shoreline development, and dissolved oxygen (DO) and AWA/LV (Table 1). Although correlation coefficients between TP and AWA/LA, and DO and AWA/LA did not reach 0.7 and -0.7, respectively, both were statistically significant (Table 1).

When two-dimensional plots were drawn on these nine combinations, Lake Akan was discriminated as an outlier in TP and AWA/LA, TP and AWA/LV, EC and AWA/LA, and EC and AWA/LV (Table 1, Fig. 2b). Lake Akan was subject to anthropogenic eutrophication in the second half of the 20th century as previously explained³⁶. We thus estimated phosphorus concentration before eutrophication. The oldest P_2O_5 data, 0.010 mg l^{-1} , measured in Lake Akan in 1931³⁷ was calculated at 0.004 mg l^{-1} phosphorus by the conversion formula which divides the value of P_2O_5 by 2.29^{10} . This result was close to the regression lines of TP and AWA/LA ($r = 0.787$, $p < 0.05$, Fig. 3a), and TP and AWA/LV ($r = 0.881$, $p < 0.01$, Fig. 3b) drawn for nine lakes except for Lake Akan. The difference (0.022 mg l^{-1}) from our observed data (0.026 mg l^{-1} , Supplementary Table S2 online) can be thought of as part of the increase from eutrophication. Without including the outlier in the case of TP and AWA, conversely, the calculation result when Lake Akan TP data was replaced by the above 0.004 mg l^{-1} drew away from the regression line ($r = 0.795$, $p < 0.05$, Fig. 3c).

A strong correlation was observed between EC and TP ($r = 0.821$, $p < 0.01$, Supplementary Table S4 online). The regression formula ($y = 819.023x - 2.343$) estimated the EC of Lake Akan at 0.933 mS m^{-1} , near the regression lines of EC and AWA/LA ($r = 0.973$, $p < 0.001$) and EC and AWA/LV ($r = 0.979$, $p < 0.001$) for the nine lakes when TP was 0.004 mg l^{-1} (Supplementary Fig. S1 online). By contrast, the calculated result of Lake Akan EC drew away from the regression between EC and AWA without the outlier ($r = 0.988$, $p < 0.001$, Supplementary Fig. S1 online), suggesting that the involvement of AWA may be invalid, along with the results of similar substitution of that between TP and AWA□

The regression line of pH and shoreline development was likewise drawn without including the outlier (Supplementary Fig. S2 online). Because shoreline development is proportional to the area of horizontal littoral zone, the correlation with pH was presumed to relate to consumption of CO_2 through hydrophytic photosynthesis^{2,5,38}.

Finally, the regression lines of DO and AWA/LA, and DO and AWA/LV were drawn with a slight negative slope due to the specific low DO data for Lake Jiro (Supplementary Fig. S3 online), and may not indicate an environmental gradient. Lake Jiro has no inflow and outflow rivers (Fig. 1a), and the water appears to be supplied through underground flow from the upstream Lake Akan³⁹. However, in addition to DO, Chl-a, DOC, and chemical oxygen demand (COD) in Lake Jiro were the

lowest concentrations among the Akan Caldera Lakes, and TP was the highest (Supplementary Table S2 online). Furthermore, a portion of the lake surface of Lake Jiro does not freeze in winter³⁹. These results suggest that other water sources, such as groundwater, may be involved in water formation in Lake Jiro

Distribution and species composition of macrophytes

We recorded 21 species of macrophytes in total (excluding emergent plants and macro algae) in 7 lakes, while no macrophyte species were observed in 3 lakes without inflow rivers (Supplementary Table S3 online). The correlation matrix of the number of macrophyte species was strong and significant with the following items among the above-mentioned lake topographic characters (Supplementary Table S4 online): boundary length ($r = 0.720, p < 0.05$), shoreline development ($r = 0.703, p < 0.05$), maximum depth ($r = 0.924 < 0.001$), mean depth (Fig. 4, $r = 0.928, p < 0.001$) and residence time ($r = 0.921, p < 0.001$). Several previous studies on relatively shallow or small lakes and ponds reported that the number of macrophyte species is correlated with lake area and that MacArthur and Wilson's "the theory of island biogeography", which theorizes how larger islands have more species than smaller islands, is often applicable⁴⁰⁻⁴⁷. However, in our study no significant correlation was found between lake area and the number of macrophyte species (Supplementary Table S4 online). The boundary length and the shoreline development are parameters affecting horizontal length of the littoral zone, and the magnitude of the maximum and mean depths and the residence time related to depth and volume of lake basin contribute to expansion of vertical littoral zone under conditions of greater water clarity. Therefore, the number of macrophyte species in the large lakes of Akan Caldera is presumed to be more closely related to the area of littoral zone than the lake area.

The two-dimensional plots of the number of macrophyte species and the above five topographic characters showed that Pond Junsai, a dystrophic lake, was designated an outlier (Fig. 4). Furthermore, when the individual species was classified as submerged, floating-leaved and free-floating, the correlation coefficient was significantly greater with the number of species of submerged plants (Supplementary Table S4 online). The number of species of floating-leaved and free-floating plants showed significant and strong correlation with the water quality parameters Chl-a, DOC, COD and TN (Supplementary Table S4 online), with most of these species localized in Pond Junsai. Thus, we conducted a cluster analysis to understand species composition of macrophytes in each lake (Fig. 5). The cluster was firstly divided into two groups: 6 species of floating-leaved and free-floating plants of Pond Junsai, and 14 submerged and 1 floating-leaved plants in the other lakes. Pond Junsai contained some indicator species of the dystrophic water: *Brasenia schreberi* (Fig. 6), *Nuphar pumila* var. *pumila*, *Nymphaea tetragona* var. *tetragona* and *Utricularia macrorhiza*⁴⁸. The remaining species recorded from the other lakes were classified as oligotrophic, mesotrophic, oligo-mesotrophic and oligo-meso-eutrophic groups (Fig. 5), following the lake-type based on the trophic status (Fig. 2a). *Ranunculus nipponicus* var. *submersus* (Fig. 6), *Potamogeton alpinus* and *Isoetes asiatica*, typically found in more pristine water^{48,49}, were designated oligotrophic. *Myriophyllum spicatum* (Fig. 6), *Hydrilla verticillata*, *Potamogeton compressus*, *Potamogeton pectinatus* and *Ceratophyllum demersum*, occurring in more eutrophic settings^{48,49}, were designated oligo-mesotrophic. *Potamogeton crispus* (Fig. 6), distributed in a variety of water environments⁴⁸, was designated mesotrophic.

As mentioned above, prior to anthropogenic eutrophication, the phosphorus level in the first half of the 20th century in Lake Akan appears to have been much lower than it is currently (Fig. 3). Thus, the current aquatic flora was also compared with results from the oldest known vegetation survey conducted in 1897⁵⁰. Of the ten species of macrophytes in Lake Akan observed in our study, nine species were also found in the 1897 list, except for *Potamogeton crispus*, classified as mesotrophic. However, the two oligotrophic species *R. nipponicus* var. *submersus* and *I. asiatica* in the old list were not confirmed. These results suggest that the species composition may have changed to a more eutrophic vegetation type

Specificity of Akan Caldera Lakes

To summarize the results, the lakes of Akan Caldera having the same origin, have developed into a series of oligotrophic, mesotrophic, eutrophic and dystrophic lakes, after being divided by a volcanic eruption (Fig. 2a). The trophic level of each

lake indicated by TP was closely related to the ratio of watershed area (AWA) to lake size (LA and LV) (Fig. 2b). These results strongly suggest the possibility that the rate of eutrophication was different among the lakes, and we see the various stages of lake succession in progress in this system. However, the observed TP of Lake Akan and its downstream neighbors, Lake Jiro and Lake Taro, are assumed to have been impacted by anthropogenic eutrophication in the past (Fig. 3a, b). Furthermore, the formation history of the Akan Caldera Lakes suggests that Ponds Hyotan and Junsai are significantly older than the other lakes²⁸⁻³⁰, and an influence of the time lag on TP among lakes must also be taken into account. To understand the loading rate of TP and its long-term fluctuation, the correct time of formation and subsequent eutrophication history of each lake should be clarified through research on lake sediment, etc. In addition, the linear regression of the relationship between TP and AWA/LA and AWA/LV (Fig. 2b) suggests that the indigenous environmental variables of the watersheds may vary little. However, in reality, the geology and vegetation within the Akan Caldera are not uniform^{28,34}, and further research is needed to determine the actual phosphorus loading from the watersheds.

Macrophyte species composition varied among lakes, driven by lake trophic conditions (Fig. 5), and is indicative of aquatic plant succession, or "hydrarch succession". Many species of macrophytes are classified into a variety of "types" according to trophic level of the habitats^{44,49,51-55}. Schneider and Melzer⁵⁵, for example, proposed seven categories ranging from oligotrophic to eutrophic and even polytrophic types. Meanwhile, Lacoul and Freedman⁴⁹ simplified into three categories: oligotrophic, eutrophic, and general types, based on the opinion that many macrophytes generally have a broad ecological range, occurring over wide trophic levels, while other species have a narrower distribution. In our study, however, all of the observed species belonged to only one of the five occurrence types, with a species-specific range of trophic level (Fig. 6). Thirteen species were distributed among oligotrophic, mesotrophic and dystrophic lake-types, respectively, and eight species occurred in the oligotrophic and mesotrophic, and the oligotrophic, mesotrophic and eutrophic type lakes with wider trophic ranges. These results explain how the species composition of macrophytes in the Akan Caldera Lakes with different trophic types is determined by the combination of species with different trophic requirements. Importantly, we noted vegetation changes in Lake Akan due to anthropogenic eutrophication: this was characterized by disappearance of oligotrophic type species, appearance of mesotrophic type species, and survival of oligo-mesotrophic and oligo-meso-eutrophic type species, when the trophic level of Lake Akan shifted from oligotrophic to mesotrophic as shown in Fig. 6. This might be the first to clearly and simply illustrate the change of species composition in aquatic plant community caused by the change of trophic level. Further investigation is necessary to test whether this is a universal phenomenon in limnology.

Trophic levels are not the only factor known to affect macrophyte distribution and species composition. Within some relatively small areas, the following physical factors have been important in producing environmental gradients between or within lakes: topography, geological qualities, inflow waters as physical factors in the watershed, lake basin morphology (mainly depth and area), water temperature, light conditions, turbidity, current flow, substrate (sediment). Chemical factors in play include inorganic ions, salinity, organic matters, conductivity, alkalinity, pH and nutrients^{12,15,24,42,44,47,49,51,52,56-60}. As this itemization indicates, a comprehensive understanding of the mechanisms that determine the distribution and species composition of macrophytes is difficult, due to multiple influencing factors. In the Akan Caldera Lakes, species distribution was related to trophic conditions (Figs. 5 and 6), while number of species was closely related to lake size (Fig. 4). Lakes Akan, Panke and Penke, all large and oligo/mesotrophic lakes with high species count, appear to offer a large variety of the physical and chemical factors noted above. The topography of capes, bays and islands in these lakes diversifies wave action and substrate via varying wind-wave parameters, and "fetch", i.e. the length of the lake surface over which wind blows^{5,49}. Inflow rivers locally alter substrate, current and water quality, greater water depth lowers water temperature and reduces substrate grain size, and oligo/mesotrophic water allows sunlight to penetrate deeper into the littoral zone, leading to a gradual gradient in the light environment^{5,6,24,43,44,47,49,57,60}. This environmental variability may offer habitat for a number of macrophytes in these large lakes. On the other hand, Pond Junsai, dominated by floating-leaved and free-floating plants, is the only example of dystrophic water quality in Akan Caldera Lakes. Its brownish lake water, derived from high DOC containing abundant humic substances, suppresses submerged plant growth due to high light absorption^{6,24,44,49,60}. Humic substances are thought to originate from decomposing terrestrial and/or littoral plant material^{6,25,38,49}. Thus,

eutrophication in Pond Junsai may have undergone a different process than in the other lakes because of differing surrounding vegetation, even if the initial process was the same. To understand the factors affecting plant distribution the relationships between detailed macrophyte distribution and habitat micro-environments in each lake, including impacts of the surrounding vegetation, must be elucidated.

Conclusion

The Akan Caldera Lakes developed environmental diversity due to a variety of lake and watershed sizes brought about by unique volcanic activity²⁸⁻³⁰. In this paper, this diversity is displayed as two orderly series of changes in trophic levels and aquatic vegetation among the lakes, possibly illustrating lake ecological succession in "real time", previously thought impossible to see^{2,9,21,26}. Odum¹⁸ called such observable examples of a coincidental series of ecological succession events in nature a "natural laboratory of succession". He further stated that "these areas not only have a priceless natural beauty, but they also constitute a natural 'teaching laboratory' in which the 'visual display' of ecological succession is dramatic". In that sense, the Akan Caldera Lakes can be seen as a massive experiment conducted by nature in "Akan Caldera Laboratory", or seen as catalog visualizing a freshwater ecosystem, focusing on lake and hydrarch succession. These fortunate coincidences have also led to attainment of conservation as a national park, so that the lakes and watershed have escaped severe disturbance from human activities, with the exception of Lake Akan^{34,36}. The well-preserved natural environments of the Akan Caldera Lakes will enable a new study approach: how lakes and aquatic organisms situated in different succession stages have responded to changes in the surrounding environment, including climate change, now seen as an issue of paramount importance²⁶.

Methods

Topography of lakes and watersheds

Lake area and boundary length were calculated using ARCGIS10 (Esri Japan Co.) based on the 1/25,000 numerical map data of the Geographical Survey Institute, Japan. Land area includes island areas.

Land watershed area was computed using the DEM10m data of the Geographical Survey Institute. After altitude data were changed into raster (altitude grid), subtle undulations were removed by the Fill tool, and bearing azimuth of flow was computed by the Flow Direction tool (north; 64, northeast; 128, east; 1, southeast; 2, south; 4, southwest; 8, west; 16 and northwest; 32). Accumulation value (number of cells accumulated toward the direction of flow) computed by the Flow Accumulation tool was extracted at accumulation values more than 30000 (sl30000) and more than 200 (sl200) by the Reclass command, and each watershed (ws30000, ws200) was computed by being grouped by every feeder of sl30000 and sl200 by the Stream Link tool. Finally, the Ws raster was converted into the polygon, and Ws30000 and ws200 were manually divided as a watershed for each lake, observing the DEM.

Lake volume and mean depth were calculated based on lake charts. Depth sounding for chart drawing was performed in autumn of 2014 in eight lakes, excepting Lakes Akan, Panke and Penke which already have lake charts. The whole lake was uniformly measured by a GPS fish finder (Lowrance HDS-8, Navico) on a motor boat. Elevation of the lake surface was obtained by the GNSS survey. The depth-sounding data were converted into contour drawings by chart drawing software, Reefmaster (ReefMaster Software Ltd.). Residence time was calculated with annual rainfall at 1200 mm³⁴.

Water quality

Measurements of physical and chemical variables and collection of lake water were performed in ten lakes of Akan Caldera from October to November 2013 and in July 2014. Electrical conductivity (EC) and pH were directly recorded using portable sensors at the center of each lake. Water was collected at the same point using 2 l polycarbonate bottles and taken immediately to the laboratory. Dissolved oxygen (DO) and chemical oxygen demand (COD) were measured by titration with

standard sodium thiosulfate solution and potassium permanganate solution, respectively. Total nitrogen (TN) and total phosphorus (TP) were measured by an auto analyzer (AACS-II, Bran + Luebbe Ltd.). Additionally, an aliquot of the water sample was filtered onto Whatman GF/F glass fiber filters, and suspended solids (SS) measured gravimetrically after drying at 110°C for two hours. Chlorophyll-a (Chl-a), concentrated onto a Whatman GF/F glass filter, was quantified with a spectrophotometer (UV-1600, Shimadzu Co. Ltd.) after extraction using methanol (100%). The filtrate was used for measuring dissolved organic carbon (DOC) with a TOC meter (TOC VC, Shimadzu Co. Ltd.).

Macrophyte survey

Macrophytes were surveyed and collected by SCUBA diving or snorkeling along the entire shorelines of Lake Akan (August and October 2012), Lake Panke (August 2012 and July 2014) and the other eight lakes (October–November 2013 and July 2014). The maximum depth surveyed was 18 m in Lake Panke.

Statistical analysis

A total of 30 variables were analyzed: 11 variables of the lake topographic factors (elevation, boundary length, lake area [LA], shore line development, maximum depth, mean depth, lake volume [LV], residence time, land watershed area [LWA], total watershed area [TWA] which is sum of LA and LWA, and accumulated watershed area [AWA] which is sum of the TWA above a given lake), 6 variables reflecting gauges of inflow and outflow of materials (LWA-LA ratio, LWA-LV ratio, TWA-LA ratio, TWA-LV ratio, AWA-LA ratio, AWA-LV)⁴, 9 variables of water chemistry (DO, pH, EC, SS, TN, TP, Chl-a, DOC, COD), and 4 variables of the macrophyte communities (number of submerged species, floating-leaved species, free-floating species and total species).

A correlation matrix of these standardized data was made and variables with strong correlation coefficients ($|r| \geq 0.7$) were investigated in detail. In lakes where macrophytes occurred, the presence/absence of individual species was converted into 1/0 data, and a cluster analysis was conducted by the Ward method using the Euclid distance. The BellCurbe (Social Survey Research Information), an add-in program for Excel, was used for the analysis.

Declarations

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Author contributions

I.W., Y.K. and J.U. drafted the manuscript. I.W. designed the study. I.W., Y.T., Y.S., H.Y. and Y.O. obtained the data. K.W. and T.H. surveyed the formation process of the lakes. I.W. analyzed the data. M.O. supervised and administrated the project. All authors discussed the results, contributed critically to the drafts, and give final approval for publication.

The authors declare no competing interests.

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Figures

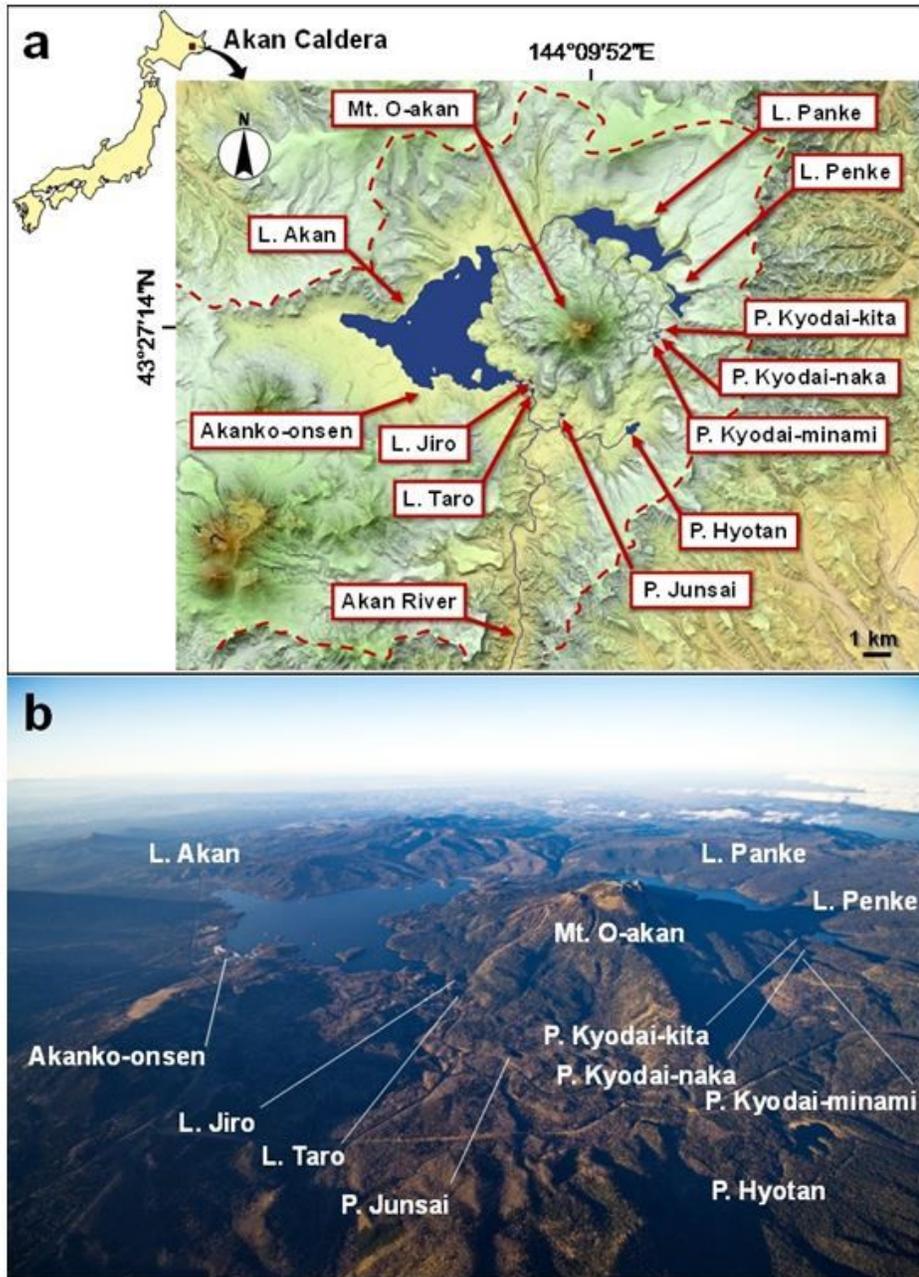


Figure 1

Map (a) and landscape (b) of Akan Caldera Lakes. The map for Akan Caldera Lakes was generated by a map software, Kashmir 3C61. The watershed of Akan Caldera is isolated by a caldera wall shown by red dotted lines in (a), but the western caldera wall is obscured by volcanos erupting after the formation of the caldera. Ten lakes surround Mt. O-akan within the caldera, and are connected by rivers and underground flow from water systems to the north and south. The water flows converge south of Mt. O-akan and discharge is through the Akan River. Land area is mostly covered with subarctic forests except for a town south of Lake Akan, Akanko-onsen. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

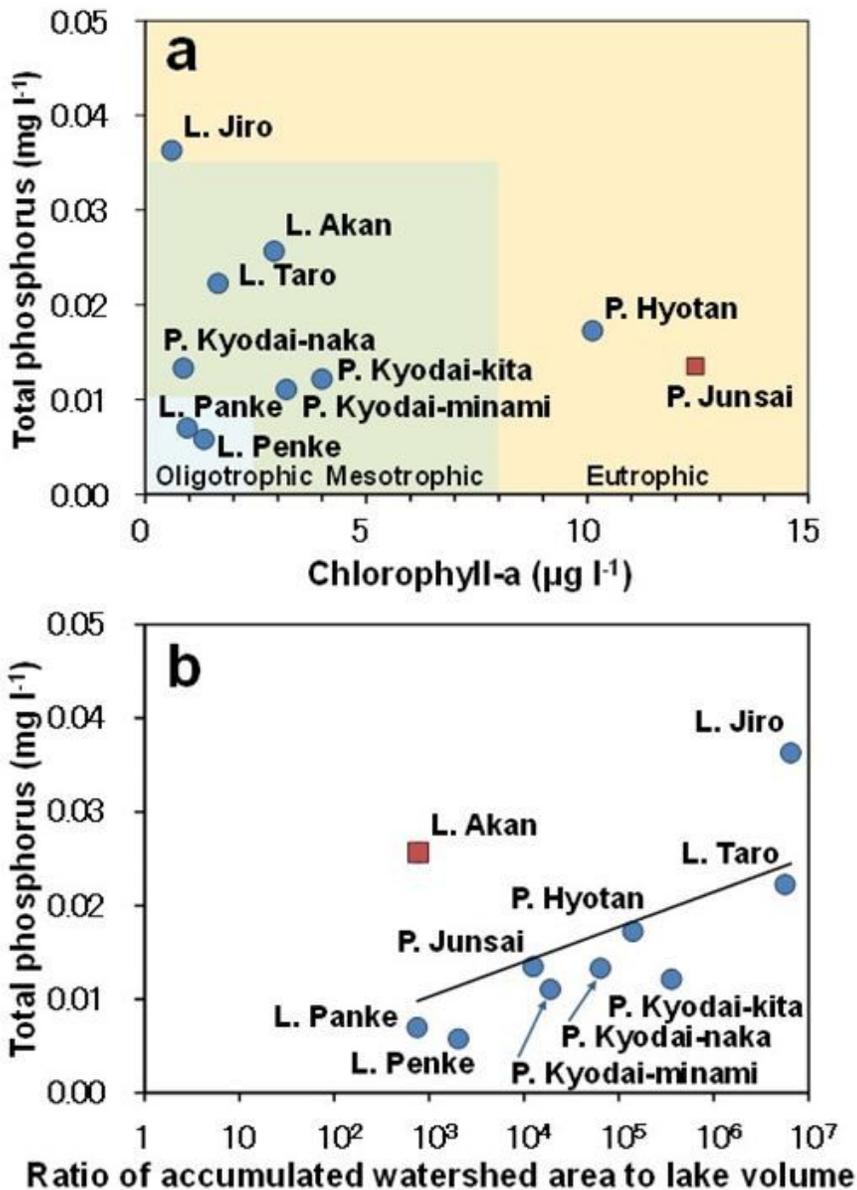


Figure 2

Aspects of trophic conditions in Akan Caldera Lakes. (a) a variety of lake types categorized by Chlorophyll-a and total phosphorous (TP) according to the Organization for Economic Co-Operation and Development (OECD)³. Even though the lakes share the same origin and most of them were formed at the same time, the lake types are diversified into oligotrophic, mesotrophic and eutrophic. Additionally, Pond Junsai (red square) has dystrophic characteristics (Supplementary Table S2 online). (b) relationship between ratio of accumulated watershed area to lake volume (AWA/LV) and TP. The AWA/LV shows significant correlation with TP thought to be a parameter of eutrophication rate, but only Lake Akan (red square) is discriminated as an outlier. Similar results are found for accumulated watershed area to lake area (Table 1, Supplementary Table S1 online). High TP specifically observed on Lake Akan is regarded as an effect of past anthropogenic eutrophication.

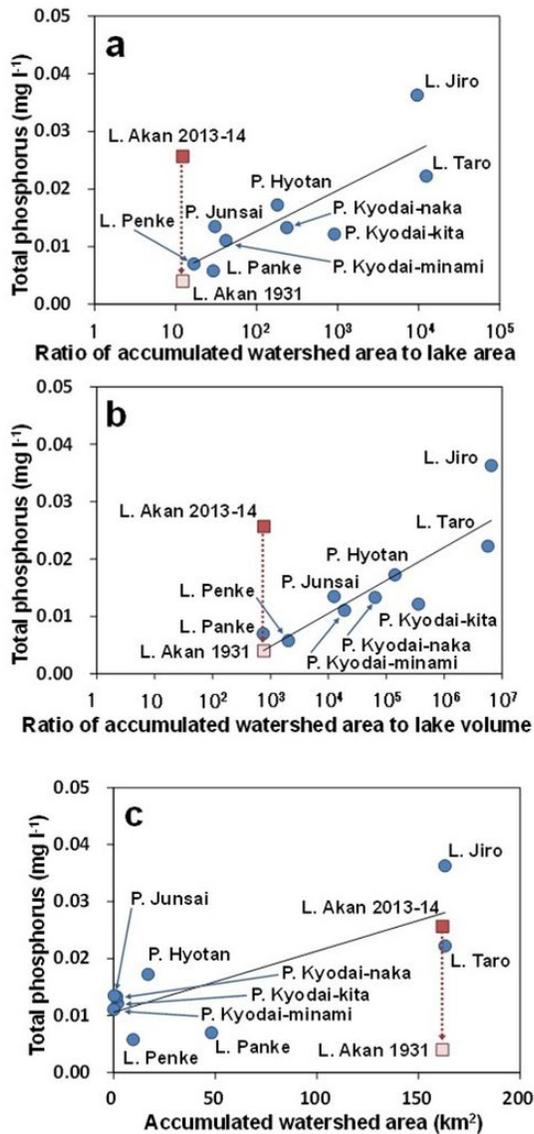


Figure 3

Estimation of phosphorus concentration in Lake Akan before eutrophication. Because Lake Akan was subject to anthropogenic eutrophication in the second half of the 20th century³⁶, phosphorus concentration before eutrophication was estimated based on the oldest P205 data measured 1931³⁷. Each regression line is drawn for nine lakes of Akan Caldera Lakes (blue circles) except for Lake Akan. In (a) relationship between ratio of accumulated watershed area (AWA) to lake area and total phosphorus (TP), and in (b) relationship between ratio of AWA to lake volume and TP, the 1931 estimate of phosphorus concentration for Lake Akan (light red square) is significantly lower than the 2013–14 TP data (dark red square), and is close to the regression lines. Conversely, in (c) the relationship between AWA and TP, the same 1931 estimate is distant from the regression line.

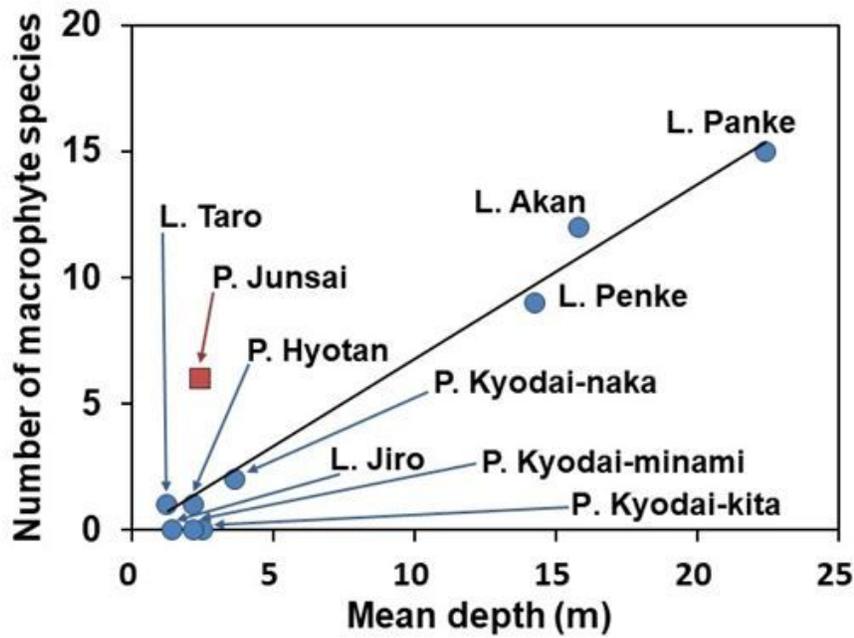
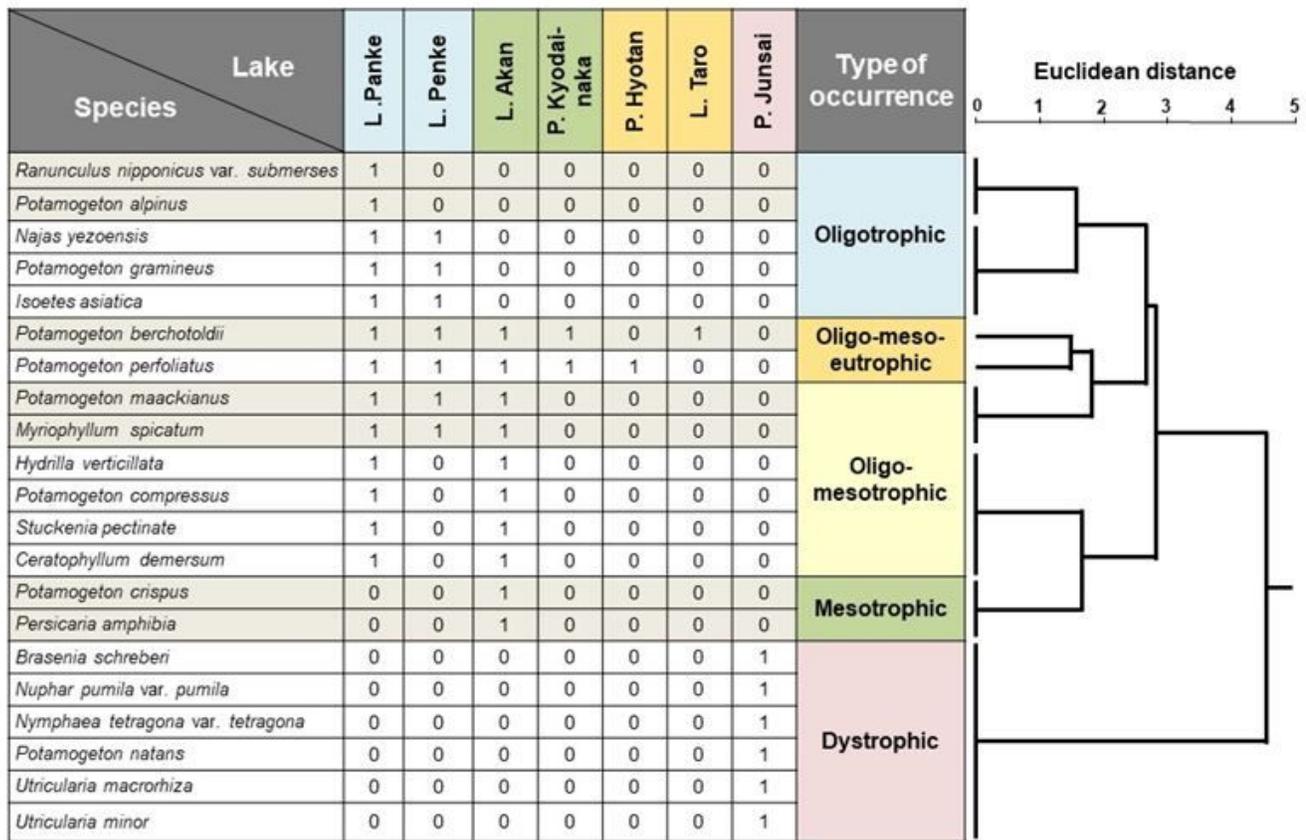


Figure 4

Effect of lake size on number of aquatic macrophyte species in Akan Caldera Lakes. In total, 21 species were observed in 7 lakes. The number of species in each lake shows high correlation with mean depth as well as with maximum depth, boundary length, shoreline development and residence time (Supplementary Table S4 online). Pond Junsai (red square) discriminated as an outlier, has a dystrophic water quality (Supplementary Table S2 online) and is dominated by floating-leaved and free-floating plants, whereas most other lakes have a submerged plant community (Fig. 5).



1: presence, 0: absence.

Figure 5

Cluster analysis of distribution and species composition of aquatic macrophytes in Akan Caldera Lakes. The tree diagram was drawn by Ward method using Euclid distance based on the 1/0 data converted from the presence/absence data for the seven lakes where macrophytes occurred. According to the lake habitat types (see Fig. 2a), clusters are classified into the five vegetation types: oligotrophic, mesotrophic, oligo-mesotrophic, oligo-meso-eutrophic, and dystrophic.

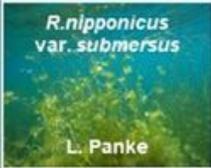
Occurrence type of macrophyte	Species of macrophyte	Trophic type of lake			
		Oligotrophic	Mesotrophic	Eutrophic	Dystrophic
Oligotrophic	<i>Ranunculus nipponicus</i> var. <i>submersus</i> <i>Potamogeton alpinus</i> <i>Najas yezoensis</i> <i>Potamogeton gramineus</i> <i>Isoetes asiatica</i>	 L. Panke			
Mesotrophic	<i>Potamogeton crispus</i> <i>Persicaria amphibia</i>		 L. Akan		
Oligo-mesotrophic	<i>Potamogeton maackianus</i> <i>Myriophyllum spicatum</i> <i>Hydrilla verticillata</i> <i>Potamogeton compressus</i> <i>Stuckenia pectinata</i> <i>Ceratophyllum demersum</i>	 L. Panke	 L. Akan		
Oligo-meso-eutrophic	<i>Potamogeton berchtoldii</i> <i>Potamogeton perfoliatus</i>	 L. Penke	 P. Kyodai-naka	 P. Hyotan	
Dystrophic	<i>Brasenia schreberi</i> <i>Nuphar pumila</i> var. <i>pumila</i> <i>Nymphaea tetragona</i> var. <i>tetragona</i> <i>Potamogeton natans</i> <i>Utricularia macrorhiza</i> <i>Utricularia minor</i>				 P. Junsai

Figure 6

Determination model for macrophyte species composition corresponding to trophic types in Akan Caldera Lakes, with representative under-water views. Individual macrophyte species belong to any one of the five occurrence types of macrophytes, accompanied by inherent trophic type(s) and range. Macrophytes of oligotrophic-, mesotrophic- and dystrophic-occurrence types are only distributed into oligotrophic-, mesotrophic- and dystrophic-type lakes, respectively. In contrast, of oligo-mesotrophic- and oligo-meso-eutrophic-occurrence types, macrophytes are able to occur widely in oligotrophic/mesotrophic- and oligotrophic/mesotrophic/eutrophic-type lakes. Accordingly, species composition of macrophytes in oligotrophic- and mesotrophic-type lakes is determined by combination of the occurrence types, oligotrophic/oligo-mesotrophic/oligo-meso-eutrophic and mesotrophic/oligo-mesotrophic/oligo-meso-eutrophic. In eutrophic and dystrophic lakes, oligo-meso-eutrophic- and dystrophic-occurrence types are distributed, respectively.

Supplementary Files

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