

# ECOLOGICAL RISK-BENEFIT ANALYSIS OF A WETLAND DEVELOPMENT BASED ON RISK ASSESSMENT USING 'EXPECTED LOSS OF BIODIVERSITY'<sup>1</sup>

TOSIHIRO OKA<sup>2</sup>, HIROYUKI MATSUDA<sup>3</sup> and YASURO KADONO<sup>4</sup>

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## Contents

<b>1</b>	<b>Introduction</b>	<b>2</b>
<b>2</b>	<b>Backgrounds</b>	<b>2</b>
2.1	From Human Health to Ecological Risk	2
2.2	Measurement of Biodiversity	2
2.3	Nakaikemi Wetland	3
<b>3</b>	<b>The Measure of Expected Loss of Biodiversity and Its Application</b>	<b>4</b>
3.1	Proposed Measure of Biodiversity	4
3.2	Realistic Measure of Biodiversity	6
3.3	Estimation of the Increase in the Probability of Extinction	8
3.4	Application to Nakaikemi Wetland	10
3.4.1	Extinction Probabilities	10
3.4.2	Contributions to Biodiversity	11
3.4.3	Expected Loss of Biodiversity	12
<b>4</b>	<b>Benefits from the Development of Nakaikemi Wetland and Risk/Benefit Analysis</b>	<b>13</b>
4.1	Treatment of the Conservation Area	13
4.2	Risk/Benefit Analysis: When the Conservation Area is Regarded as Maintaining the Diversity	13
4.3	Risk/Benefit Analysis: When the Development is Regarded as Causing Loss of All the Biodiversity of the Wetland	13
<b>5</b>	<b>Discussion</b>	<b>14</b>
5.1	How to Use the Result	14
5.2	Extinction in Japan and Worldwide Biodiversity	14
5.3	What Aspects of Ecological Risk are Excluded from ELB?	14

**Key Words:** probability of extinction, taxonomic diversity, risk-benefit analysis, wetland, ecological risk

<sup>1</sup>Work supported by CREST of the Japan Science and Technology Corporation.

<sup>2</sup>Associate Professor, Faculty of Economics, Fukui Prefectural University, 4-1-1 Kenjojima, Matsuoka, Yoshida, Fukui 910-1195, Japan; CREST, Japan Science and Technology Corporation.

<sup>3</sup>Associate Professor, Ocean Research Institute, The University of Tokyo, 1-15-1 Nakano-ku, Tokyo 164-8639, Japan; CREST, Japan Science and Technology Corporation.

<sup>4</sup>Associate Professor, Department of Biology, Faculty of Science, Kobe University, 1-2-1 Tsurukabuto, Nada, Kobe 657-8501, Japan.

# 1 Introduction

Quantitative risk assessment has been well-established so far as adverse effects of environmental pollution on human health are concerned, and risk management based on quantitative risk assessment is becoming more and more widely used in policy-making. Quantitative risk assessment is also needed for the ecological effects of environmental degradation in order to ensure that the management of the ecosystem is based on more rational grounds. In this paper we present a new method of assessing the ecological risk by using the index of ‘expected loss of biodiversity (ELB)’. ELB is defined as the weighted sum of the increments in the probabilities of extinction of species that would be caused by human activities such as land-use conversion or pollution. With regard to the weighting for a particular species, this is calculated according to the length of the branch on the phylogenetic tree that will be lost if the species becomes extinct. We have applied this method to a case of land-use conversion of Nakaikemi Wetland in Japan. The result has been combined with the economic benefits from the development of the wetland, so as to produce an indicator of cost-effectiveness, i.e., ‘cost per ELB’ of the conservation of the wetland.

In section 2, backgrounds of this study are presented. In section 3, it is shown how the index of ‘expected loss of biodiversity (ELB)’ is constructed and applied to the case of the development of Nakaikemi. In section 4, the benefits from the development, or the costs for conserving the wetland are estimated. In section 5, the results are discussed.

## 2 Backgrounds

There are two backgrounds to our study. One is the need for expanding the framework of risk assessment from human health risks to ecological risks. The other is the need for a measure of biodiversity that can be used in policy appraisal.

### 2.1 From Human Health to Ecological Risk

One reason why ecological risk assessment is not so well-established as human health risk assessment is that an appropriate endpoint has not been determined. In human health risk assessment, ‘death’ of individual human beings is most widely adopted as the endpoint for risk assessment, and risk is expressed in terms of the probability of death or of the indicator closely linked with the probability of death such as loss of life-expectancy. As Nakanishi (1995, 1997) points out, the success of health risk assessment is indebted to the fact that the endpoint is the event that everyone wants to avoid. To the contrary, in ecological risk assessment, various endpoints are adopted, most of which are not unanimously wanted to avoid. For instance, one may accept death of some individuals of a particular animal species, or one may accept loss of a habitat of some populations of several plant species.

Nakanishi (1995, 1997) proposed to adopt the extinction of species as the endpoint for ecological risk assessment, in that the extinction must be an event that everyone wants to prevent. Our study is an attempt to actualize this proposal.

### 2.2 Measurement of Biodiversity

Conservation of local ecosystems has been treated as a separate issue from conservation of global biodiversity. It is certainly easy to envisage that the existence of local ecosystems contributes to global biodiversity, but it has been the intrinsic values of a local ecosystem that have pushed forward its conservation.

When the biodiversity of local ecosystems is concerned, it is often measured by an indicator which can be defined within the ecosystem independently from the world outside of it. The number of species present on a certain area of land, for instance, is often used as a measure of diversity. This can be defined independently from the world outside of the land.

Our study is an attempt to combine the issue of local ecosystems with that of global biodiversity. We have developed a measure for the contribution of a particular local ecosystem to global biodiversity.

### 2.3 Nakaikemi Wetland

The case to which we are attempting to apply our method of ecological risk assessment is the development of Nakaikemi Wetland.

Nakaikemi Wetland (Tsuruga, Japan) is a wetland of about 25 ha, which is characterized by its unique geomorphic feature of pouched valley aggraded with mud (Fig.1). Most of the area has been used as rice paddy for hundreds of years but recently more than two third of the land lie fallow according to a set-aside policy because this area has the lowest rice-growing productivity. Abandoned rice fields have been found to support a remarkable biodiversity.

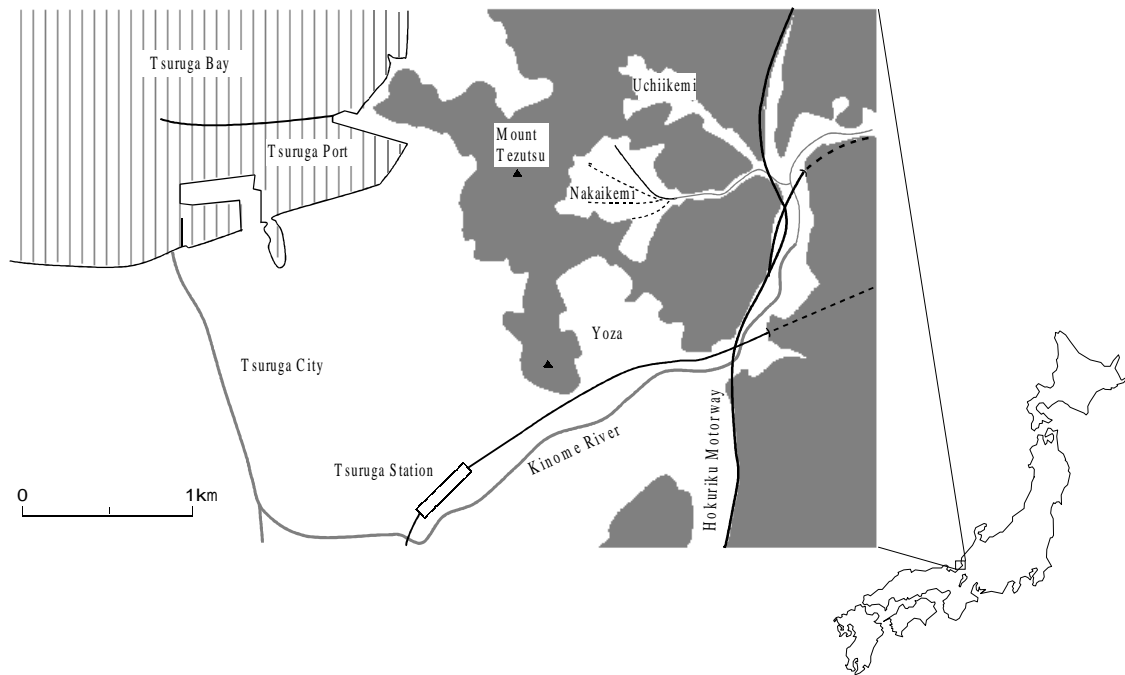


Figure 1: Nakaikemi Wetland

In this area live many species of aquatic plants which are regarded as declining nationwide, including 13 of the ‘threatened’ and 2 of the ‘nearly threatened’ plant species according to the Red List published by the Japanese Environment Agency in 1997. There are also many species of fish including ‘threatened’ cyprinodont and insects including more than 60 kinds of dragonflies and several kinds of declining diving beetles.

Osaka Gas Company made a plan for the construction of a liquefied natural gas (LNG) plant on this area in 1992. The procedure for the environmental impact assessment was completed in 1996, whereby the plan was allowed on condition that threatened and rare plant species be transplanted to the ‘protected conservation area’ of 3.3ha and that a transplantation test be conducted for three years.

A protection movement opposed to the development plan was organized as soon as the plan was made public. The Ecological Society of Japan issued a statement calling for the preservation of the whole area of this wetland in 1996.

Osaka Gas Company argues that the natural life on this wetland is a secondary one created as a by-product of human cultivation, that the diversity of this land will be reduced if left to nature, and that, therefore, the protection of the ‘conservation area’ is necessary for the natural life on this land. Ecologists oppose this argument by asserting that the transplant will not succeed owing to the complexity of the relationship among the species living in the wetland, that no one can judge the success of the transplant in three years, that human-controlled nature in such a small area is not the same as what

existed before, and that, therefore, the whole area should be conserved for the traditional utilization of the land (Kadono, 1997).

### 3 The Measure of Expected Loss of Biodiversity and Its Application

#### 3.1 Proposed Measure of Biodiversity

Biodiversity is a broad concept that can contain hierarchical definitions of various levels. It is said to be defined at the level of gene, species, ecosystem and landscape (Washitani and Yahara, 1996, p.38). The diversity of ecosystem or landscape is, however, elusive and yet to be more refined for operational measurement. Here we adopt the biodiversity of species as a first approximation.

How to measure the species diversity? It is said that since the existing diversity of species is the product of the accumulation of speciations having taken place for a very long time, and a speciation, in turn, is a process of trial and error of natural genetic modification taking millions of years, loss of a species is equivalent to loss of cultural heritage of tens of millions of years (Washitani and Yahara, 1996, p.95).

The phylogenetic tree can be regarded as a record of the history of speciations. It is quite understandable, therefore, that the idea of developing an indicator of biodiversity by means of phylogenetic information.

The first attempt was made by Vane-Wright, Humphries and Williams (1991). They regarded the reciprocal of the number of nodes between a particular taxon and the root of the phylogenetic tree as representing the contribution of the taxon to global biodiversity. In the tree shown in Fig. 2, if

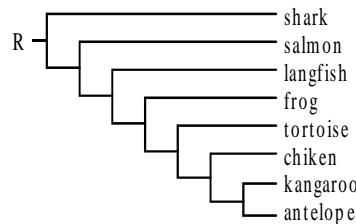


Figure 2: Contribution of taxa to diversity—root-weighting—

the contribution to diversity of shark is 1, then that of salmon is 1/2, that of frog is 1/4, and that of kangaroo or antelope is 1/7. The nearer to the root, the larger the contribution to diversity of a taxon. This approach was called later ‘root-weighting’.

They, however, was not satisfied with this measure, because it is flawed when it is used for ‘unresolved trees’. In the tree shown in Fig. 3, for instance, every taxon has an equal weight in the root-weighting

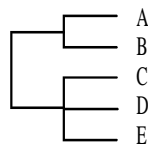


Figure 3: Root-weighting in an unresolved tree

method, but if two taxa should be chosen, one should be chosen from A and B and the other from C, D and E in order to conserve more diversity (Williams et al., 1991, p.668).

Assigning this flaw for weighting individual taxa, Williams et al. (1991) pursued methods using pairwise measurement of the relative divergence between two taxa. They presented four kinds of pairwise measure using the number of shared nodes between two taxa ( $S_{ij}$  for taxa  $i$  and  $j$ ) and the number of unique nodes for a taxon  $i$  with respect to another taxon  $j$  ( $U_{ij}$ ), and by using these measures, they developed a criterion of taxonomic dispersion.

The first pairwise measure is  $\sum 1/S_{ij}$ . In the problem of selecting three among the eight taxa in Fig 2, this measure selects shark, salmon and one of the other species. The second pairwise measure they developed is  $\sum(U_{jk} + U_{kj} + 1)$ , under which shark, { kangaroo or antelope } and one of the others are selected. The third measure is  $\sum(U_{jk} + U_{kj} + 1)/(2S_{jk} + U_{jk} + U_{kj})$ , under which shark, salmon and { kangaroo or antelope } are selected. The fourth is  $\sum(U_{jk} + U_{kj})/S_{jk} + 1$ , under which shark, frog and { kangaroo or antelope } are selected.

The dispersion criterion proposed by Williams et al. (1991) is

$$\text{number of spp.} \times [\text{mean divergence}(U_{ij} + U_{ji} + 1) - \text{s.d. of divergences}]$$

Under this dispersion criterion, the selection of shark, frog and { kangaroo or antelope } has the largest diversity. They applied the last criterion to setting priority to the habitats of bumble bees (the sibilicas group of *Bombus*) in the world (Williams et al., 1991, 1993).

Weitzman (1992) revealed that any measure of diversity based on *ultrametric* distance can be represented by length of the branches of a phylogenetic tree. ‘*Ultrametric*’ means that the distance between a terminal node and the root node is equal for every terminal. He investigated under what conditions a non-ultrametric distance can generate a measure of diversity having desirable properties. Total diversity of a group of species is represented by the total length of the branches of the taxonomic tree for the group, and the distance between any two species in the tree is depicted as the length of the branch between either of them and the node of their nearest common ancestor. The loss of diversity when a species extincts is also represented by the length of the branch between the terminal node of the species and the node of its nearest ancestor which is shared with another species.

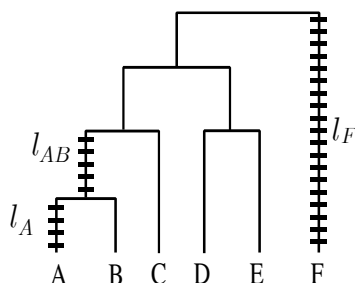


Figure 4: Weitzman's measure of diversity

For instance, in the tree presented in Fig. 4, taxon A contributes to global diversity by the length of the branch between the terminal node for A and the node representing the nearest common ancestor to A and other taxa, namely  $l_A$ . Taxon F, similarly, contribute to global diversity by  $l_F$ . Accordingly, when they become extinct, the loss of diversity is also  $l_A$  for A and  $l_F$  for F, respectively.

In this framework, the contribution to diversity of a particular taxon is independent from the scope for which total diversity is considered. The diversity of an upper taxon consisting of A and B, for example, is measured to be  $l_A + l_B$ , to which A contributes by  $l_A$ . The diversity of a still upper taxon consisting of A, B and C is  $l_A + l_B + l_{AB} + l_C$ , to which A again contributes by  $l_A$ . The loss of diversity due to the extinction of A is, therefore, always  $l_A$ , irrespective of the upper taxon for which total diversity is calculated. Extinction of other taxa, however, affects the contribution to diversity of a particular taxon. When B is extinct, for example, A's contribution will increase to  $l_A + l_{AB}$ .

Weitzman (1993) applied this measure to setting priority to the protection of the crane species of the world.

### 3.2 Realistic Measure of Biodiversity

The above proposals for the measure of biodiversity by Williams et al. and Weitzman are helpful but have common and specific problems for our purpose.

We are attempting to construct a measure of biodiversity that can be used for assessing the contribution of a particular land such as Nakaikemi Wetland. The approach of Williams et al. or Weitzman cannot be used directly for this purpose.

First, any pairwise measures of divergence between species are not suitable to our study. The pairwise measures make sense only when the whole cladogram for all the clades including relevant species is available. Williams et al. could use their pairwise measure because they had to obtain the values of their pairwise measures for only 43 species within *Bombus*. One can calculate the decrease in the value of ‘dispersion’ constructed of pairwise measures of divergence due to a loss of some species among those 43 species in one genus.

Nakaikemi has more than 1,000 animal and plant species, which belong to various genera, families, orders and so on. If, for instance, one wants to assess the impact of the extinction of *Iris laevigata*, which lives in Nakaikemi, by using Williams et al.’s approach, one will have to calculate the ‘dispersion’ for the cladogram of the genus *Iris* for the case where *Iris laevigata* exists and for the case where it does not exist. To take the genus as a clade for which the ‘dispersion’ is calculated is, however, arbitrary. One could take the family Iridaceae. Since the genus *Iris* has about 200 species while the family Iridaceae has about 1,400 species, the ‘dispersion’ becomes larger for the family than for the genus just because of the difference in the number of species contained, and hence the decrease in the value of dispersion due to the loss of a species would be larger for the family. Furthermore, Nakaikemi has species belonging to other taxa, for example, some species belonging to the genus *Sparganium*, which, in turn, belongs to the family Sparganiaceae. There is no reason, therefore, to reject taking an upper clade including both Iridaceae and Sparganiaceae, say the monocotyledon. Considering the fact that Nakaikemi has flowering plants other than monocotyledons, seed plants other than flowering plants and vascular plants other than seed plants, the only clade without arbitrariness for which the dispersion is calculated is the highest clade including all the species. To calculate the dispersion for the highest clade for all the species is, evidently, impossible.

Weitzman’s approach is free from this problem, because it can calculate the loss of diversity due to the extinction of some species independently from the choice of the clade for which total diversity is considered. This approach, however, has difficulty when it is to be used for assessing the diversity contribution of a particular land, i.e., it requires the length of branches in the phylogenetic tree. Weitzman (1993) was able to determine the length of the branches in the phylogenetic tree for 15 crane species by using the genetic distances among them estimated by DNA-DNA hybridization. Nowadays the method of comparing DNA sequences is widely used to estimate phylogenetic relationships. However, genetic distances are not always obtained from such data.

Considering those difficulties and the necessity of diversity measure for a particular land, we propose to adopt the Williams et al.’s original root-weighting but to interpret the reciprocal of the number of nodes between the root and the terminal as a surrogate for the length of the branch between the terminal node and the node of the nearest common ancestor with another species, assuming all the branches represent ultrametric distances.

In Fig. 5,  $l_i$ , ( $i = A, B, C, D$ ) represents the length of the branch between the terminal node for species  $i$  and the nearest node shared with another species. The length of the branch between the nearest shared node for  $C$  and  $D$  and the nearest shared node among  $B, C$  and  $D$  is represented by  $l_{CD}$ , and the branch length between the latter node and the nearest shared node among  $A, B, C$  and  $D$  is represented by  $l_{BCD}$ .

Our approach is to determine the values for  $l_i$ ’s as  $l_A = 1$ ,  $l_B = 1/2$  and  $l_C = l_D = 1/3$ . Assuming ultrametric distances implies  $l_{BCD} = 1/2$  and  $l_{CD} = 1/6$  in Fig. 5.

In addition to the problem of the lacking of the knowledge about real length of branches, there is another problem, i.e., a fully resolved phylogenetic tree is not always available. For some families relationships between genera have been studied well, whereas for other families not. For some genera relationships between species have been studied well, whereas for other genera not. Confronted with this problem we adopted the approach to use a phylogenetic tree from the root to a certain upper taxon including a species in question, and to estimate an expected value of the reciprocal of the number of

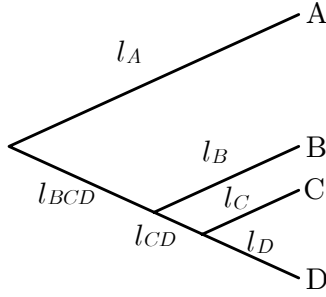


Figure 5: Measure of diversity

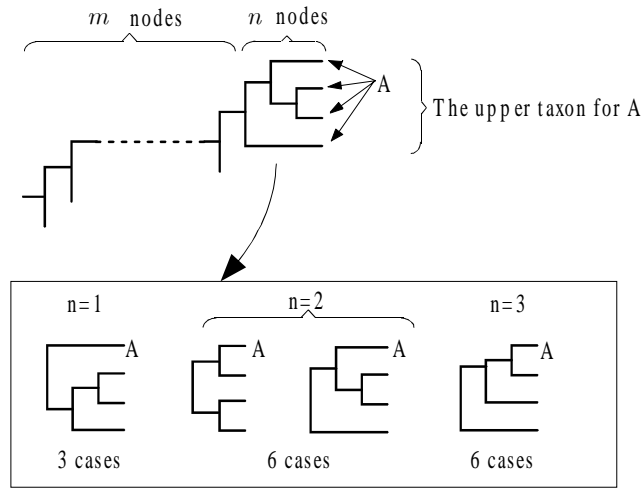


Figure 6: Node counting when there are four species in the upper taxon

nodes between the terminal node for the species and the root from the number of species included in that upper taxon.

For instance, when there are four species within an upper taxon, 15 phylogenetic trees can occur within the upper taxon. In three cases of them a species, say A, has one node between the root of the upper taxon and itself, in six cases A has two nodes between the root and itself and in six cases it has three nodes. Hence, when the upper taxon itself has  $m$  nodes between itself and the root of the whole tree (Fig. 6), the expected mean value of the reciprocal of the number of nodes between the terminal node for species A and the root of the whole tree is

$$\frac{3}{15} \times \frac{1}{m+1} + \frac{6}{15} \times \frac{1}{m+2} + \frac{6}{15} \times \frac{1}{m+3}.$$

When there are  $n$  species within an upper taxon, the number of phylogenetic trees in which a species A has  $k$  nodes between itself and the root of the upper taxon is represented by  $f_k(n)$  that meets the equation

$$\begin{cases} f_1(n) = f(n-1) \\ f_k(n) = \sum_{i=1}^{n-k} {}_{n-1}C_i f(i) f_{k-1}(n-i), \quad k = 2, 3, \dots, n-1 \end{cases}$$

where  ${}_n C_i$  is the combinations of  $n$  things taken  $i$  at a time and  $f(n)$  represents the total number of

phylogenetic trees when there are  $n$  species, i.e.,

$$f(n) = \sum_{i=1}^{n-1} f_i(n).$$

The expected mean value of the reciprocal of the number of nodes between the terminal node for species A and the root of the whole tree is, therefore,

$$E_n\left[\frac{1}{m+k}\right] = \frac{1}{f(n)} \sum_{k=1}^{n-1} \frac{f_k(n)}{m+k},$$

where  $m$  is the number of nodes between the upper taxon and the root of the whole tree.

To obtain the value of  $E_n[1/(m+k)]$  using these equations requires huge amount of calculations when  $n$  is large. Hence in practice when  $n$  is larger than 100 we used as an approximation for  $E_n[1/(m+k)]$

$$\frac{1}{m + \frac{1}{E_n[1/k]}},$$

where  $E_n[1/k]$  is equal to  $E_{n-1}[1/k](2n-4)/(2n-3)$ .

Any group of taxa can be chosen as the upper taxon, whether a family, a group consisting of two families or an order or a higher taxon, as long as the taxon is monophyletic.

Our interpretation of the root-weighting is effective to overcome its flaw for an unresolved tree pointed out by Williams et al..

For among C, D and E in Fig. 3, there are only three possible relationships shown in Fig. 7. Since C's diversity contribution is 1/2 with the probability of 1/3 and 1/3 with the probability of 2/3, the expected value of C's contribution equals 7/18. Similarly, the contribution to diversity of D or E is also

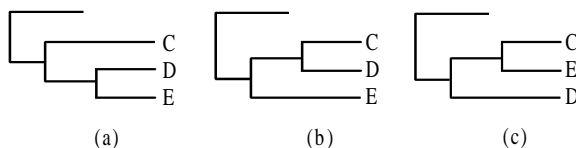


Figure 7: Possible phylogenetic relationships among three species

7/18, while the diversity contribution of A or B is 1/2. Therefore, when one has to choose one species to be extinct, he/she should choose one among C, D and E. After choosing one among them, say C, the diversity contribution of D and E increases to 1/2. As a result, if a second species should be chosen to be extinct, all the remaining species are indifferent. Suppose D is chosen, then the diversity contribution of E increases to 1. Therefore if a third species has to be chosen to become extinct, you A or B should be chosen. Consequently, one species will successfully be selected from A and B and one from C, D and E when two species are required to be preserved among the five in Fig.3.

### 3.3 Estimation of the Increase in the Probability of Extinction

The above argument concerns the impact of extinction of species on global diversity. However, we are attempting to develop an indicator of diversity that can be used for assessing the contribution to diversity of a particular land, and the loss of an ecosystem on a particular land does not usually cause extinction of any species. Our approach to assess the impact of the loss of a land is to capture its effect on the probability of extinction of the species living there.

Loss of an ecosystem on a land means loss of a habitat of the species living there. That would cause some increases in the probability of worldwide extinction of them. This increment in the extinction probability for a species multiplied by the diversity contribution of the species discussed above can be



regarded as the expected loss of the contribution to biodiversity of the species due to the loss of a habitat. The sum of those expected loss of the contribution over all the species living on the land can be called 'Expected Loss of Biodiversity (ELB)' due to the loss of the land.

Our estimate on the increases in the extinction probabilities here is limited to vascular plants and to the nationwide extinction in Japan due to the limitation of the methodology of estimation. Our method relies on the simulation used in creating the Red List for vascular plants in Japan. The Red List was created in 1997, following the categories and the criteria of IUCN's Red List of 1994, and adopted the quantitative assessment of the probabilities of extinction for each of the vascular plants (Kankyoty, 1997). Among the five criteria, the so called criterion 'E' is based on the quantitative assessment of the extinction probability. This criterion classifies the threatened species into:

- CR (critically endangered), if the probability of extinction is larger than or equal to 50% in 10 years or 3 generations,
- EN (endangered), if the probability of extinction is larger than or equal to 20% in 20 years or 5 generations, and
- VU (vulnerable), if the probability of extinction is larger than or equal to 10% in 100 years.

Actual classification was made according to the criterion that gave the most severe result among the criteria A, C, D and E.

The assessment of the extinction probabilities was made by a simulation based on the data on the number of sites where a species exists, the population size at each site and the nationwide distribution of the reduction rates of the population in the past 10 years (Yahara et al., 1998). The data were collected from about 400 researchers. The simulation assumed the distribution of the reduction rate in the past 10 years would hold in the future, and conducted 1000 trials to assess how many times a species would become extinct within the next 100 years.

This simulation produces the mean time for the extinction for each species. By using this simulation, the increment in the mean time for the extinction when one habitat is lost can be calculated.

The reciprocal of the mean time for the extinction means the probability of extinction per year, if the extinction in each year is assumed to occur independently from that in other years. If we let  $T$  represent the mean time for the extinction of a species, our proposal is to adopt  $\Delta(1/T)$  as a measure of the risk<sup>1</sup>.

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<sup>1</sup>The assumption of independency of extinction is restrictive, because the simulation of extinction itself is based on the dependency of extinction in each year on the reduction in population occurring in the previous years. However, the change in the mean time for extinction itself,  $\Delta T$ , cannot be regarded as representing appropriately the impact of the loss of a land. For, the loss of one year of the survival expectancy of the species which has 10 years of expectancy should not be the same as the loss of one year of the expectancy of the species which has 100 years of expectancy, and the impact of the latter should be regarded as smaller than that of the former. To adopt  $1/T$  as a risk measure is one way to avoid this problem.

Alternative approach is to adopt the loss in 'discounted years of existence' as a risk measure. If the discount rate is  $r$ , the 'discounted years of existence' until the year  $t$  is

$$\int_0^t e^{-rs} ds = \frac{1 - e^{-rt}}{r}.$$

Since the probability of extinction at the year  $t$  is

$$m(t) \exp \left[ - \int_0^t m(s) ds \right],$$

where  $m(t)$  is the probability of extinction in year  $t$ , the expected value of the discounted years of existence is

$$L = \frac{1}{r} \int_0^\infty m(t) \exp \left[ - \int_0^t m(s) ds \right] (1 - e^{-rt}) dt.$$

When the extinction in each years is independent and its probability is constant to be  $m$ ,  $L$  is equal to

$$\frac{1}{m + r},$$

or

$$\frac{1}{1/T + r}.$$

ELB is calculated as the weighted sum of the increments in the extinction probabilities with the weight proportionate to the contribution to diversity of the species represented as the branch length for the species. In the example in Fig. 5, suppose the increase in the probability of D is  $\Delta P(D)$ , then the loss of biodiversity will be  $l_D \Delta P(D)$ . However, when species C has the probability of extinction equal to  $P(C)$ , then the expected loss of diversity due to the increase in the extinction probability of species D by the amount  $\Delta P(D)$  should be

$$\Delta P(D)[l_D + l_{CD}P(C)]$$

rather than  $l_D \Delta P(D)$ . When A and B also have their own extinction probabilities of  $P(A)$  and  $P(B)$ , respectively, the expected loss of diversity due to the increase in the extinction probability of species D by the amount  $\Delta P(D)$  should be

$$\Delta P(D)[l_D + l_{CD}P(C) + l_{BCD}P(C)P(B)].$$

Generally, if  $A(s)$  represents the set of the branches whose both nodes are ancestors of the species  $s$  and  $S(i)$  represents the set of species one of whose ancestors are adjacent to a branch belonging to  $A(s)$ , namely

$$S(i) = \{s | A(s) \ni i\},$$

then the expected loss of diversity due to the increase in the extinction probability of species  $s$  by the amount  $\Delta P(s)$  is equal to

$$\Delta P(s) \sum_{i \in A(s)} l_i \prod_{s^0 \neq s, s^0 \in S(i)} P(s'). \quad (1)$$

Strictly speaking, this formula should be used as a measure of expected diversity loss, but the extinction probability of one of the closely related species is usually much smaller than one and the probability of simultaneous extinction of some of them is further smaller, so the members in the summation of the formula (1) other than  $l_s$  can be negligible.

## 3.4 Application to Nakaikemi Wetland

### 3.4.1 Extinction Probabilities

There exist hundreds of species of vascular plant at Nakaikemi Wetland, but to assess the increments in the extinction rates due to the loss of this land for all of those species is impossible because the data necessary for making the Red List were not collected for the species that were evidently not threatened. In fact, it is not necessary to assess the impact for all the existing species, because the impact on the extinction probability for the species that are secure must be negligible. Accordingly, we made calculations only for the species included in the categories of ‘threatened’—consisting of ‘critically endangered’, ‘endangered’ and ‘vulnerable’—or of ‘nearly threatened’ species.

The result concerning the impact of the loss of land on the extinction probabilities for the vascular plants is shown in Table 1<sup>2</sup>.

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When the probabilities of extinction until the year  $T - 1$  are zero and that for the year  $T$  is one,  $L$  becomes

$$\frac{1 - e^{-rt}}{r}.$$

The advantage of using the measure of the expected discounted years of existence is that it allows the dependency of the extinction probabilities. The disadvantage of this method is that it requires specifying the discount rate. Since the discount rate in the above equations has no relation to that in the economic sense, namely, the people’s rate of time preference, which can be observed in the market place, we have no empirical ground to determine it. The advantage of the measure  $\Delta(1/T)$  is simplicity and the fact that it does not need any discount rates, but it requires an implausible assumption that the extinctions in each years occurs independently of each other in order to allow the interpretation that it represents the extinction probability per year. However, the measure  $\Delta(1/T)$  can give us a convenience that we can use the term ‘expected loss of biodiversity’ as being represented by the product of the probability of extinction and the measure of biodiversity.

<sup>2</sup>For this calculation, it is necessary to know the number of habitats by population size and the number of habitats by rate of population decline. These figures are to be published by the *Red Data Book*. Information on the population of each species at Nakaikemi is also necessary, and this has been provided in the research done by Kadono.

Table 1: Increments in the extinction probabilities of vascular plants due to the loss of Nakaikemi

Species	Family	Red List Category	Time for extinction ( $T$ )		$\Delta(1/T)$
			Before the loss (year)	After the loss (year)	
<i>Isoetes japonica</i>	Isoetaceae	VU	89.96	89.89	$8.90 \times 10^{-6}$
<i>Marsilea quadrifolia</i>	Marsiliaceae	VU	32.32	32.26	$6.43 \times 10^{-5}$
<i>Salvinia natans</i>	Salviniaceae	VU	54.57	54.56	$5.71 \times 10^{-6}$
<i>Azolla japonica</i>	Azollaceae	VU	52.76	52.65	$4.10 \times 10^{-5}$
<i>Persicaria foliosa</i>	Polygonaceae	VU	54.00	53.87	$4.26 \times 10^{-5}$
<i>Trapa incisa</i>	Trapaceae	VU	85.08	84.06	$1.42 \times 10^{-4}$
<i>Eusteralis yatabeana</i>	Lamiaceae	VU	35.99	35.54	$3.56 \times 10^{-4}$
<i>Prenanthes tanakae</i>	Asteraceae	VU	119.59	118.87	$5.10 \times 10^{-5}$
<i>Sagittaria aginashi</i>	Alismataceae	NT	162.02	161.91	$4.38 \times 10^{-6}$
<i>Najas japonica</i>	Najadaceae	EN	37.73	37.51	$1.53 \times 10^{-4}$
<i>Monochoria korsakowii</i>	Pontedariaceae	VU	56.44	56.23	$6.68 \times 10^{-5}$
<i>Iris laevigata</i>	Iridaceae	VU	102.22	102.15	$6.32 \times 10^{-6}$
<i>Sparganium erectum</i>	Sparganiaceae	NT	185.15	185.08	$1.90 \times 10^{-6}$
<i>Sparganium japonica</i>	Sparganiaceae	NT	202.22	201.77	$1.10 \times 10^{-5}$
<i>Habenaria sagittifera</i>	Orchidaceae	VU	81.80	81.79	$1.49 \times 10^{-6}$

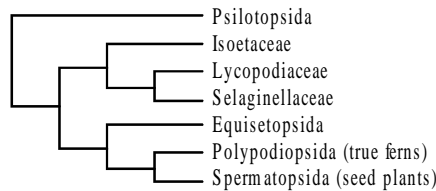


Figure 8: Phylogenetic tree for high taxa of vascular plants

The expected time for extinction of, for instance, *Marsilea quadrifolia* is 32.32 years when Nakaikemi exists. It becomes 32.26 years if this wetland disappears. Therefore, the loss of Nakaikemi will cause a loss of survival expectancy of 0.06 years.

### 3.4.2 Contributions to Biversity

The contribution of the species listed in Table 1 was calculated according to the approach discussed in section 3.

For the relationships among Psilotopsida, Lycopodiopsida, Equisetopsida, Polypodiopsida and Spermatopsida, we assume the tree shown in Fig. 8 according to Bremer et al. (1987) and Bremer (1985). The relationship among the three families of Lycopodiopsida, namely Isoetaceae, Lycopodiaceae and Selaginellaceae, is based on the molecular analysis by Manhart (1995), although the molecular analysis has not produced stable results for this level of taxa.

As a result, the number of nodes for Isoetaceae between the terminal and the root is three, which is shown in the column ‘number of nodes above the upper taxon’ for *Isoetes japonica* in Table 2.

For the true ferns, we determined the number of nodes above the families according to the molecular phylogenetic tree from Hasebe et al. (1995, p.146). We counted the nodes for the seed plants according to the phylogenetic tree presented by Chase et al. (1993) (B series of their figures). For details about the phylogenetic trees and node counting for the true ferns and the seed plants see Appendix.

We chose families as the upper taxa for which we counted the nodes between them and the root of the whole tree for the vascular plants, except for *Eusteralis yatabeana*, *Sagittaria aginashi*, *Najas japonica* and *Habenaria sagittifera*. For those four species we chose higher taxa as shown in Table 2. For the reason why we chose those taxa as the upper taxa, see Appendix.

The resulting numbers of nodes are shown in the column ‘number of nodes above the upper taxon’. The numbers for the flowering plants were not determined uniquely because the phylogenetic tree we used

Table 2: Contribution to biodiversity and ELB of the plant species in Nakaikemi

No	Species	Upper taxon	No of nodes above the upper taxon	No of species within the upper taxon	Contribution to biodiversity		ELB $\Delta P_i Y_i$ (year)
					$B_i$	$Y_i$ (year)	
1	Isoetes japonica	Isoetaceae	3	68	0.07332	29328994	261
2	Marsilea quadrifolia	Marsiliaceae	9	67	0.04879	19514737	1254
3	Salvinia natans	Salviniaceae	10	10	0.07070	28278915	161
4	Azolla japonica	Azollaceae	10	6	0.07720	30881499	1267
5	Persicaria foliosa	Polygonaceae	20-21	1000	0.01775	7101914	303
6	Trapa incisa	Trapaceae	25-29	15	0.03085	12341354	1755
7	Eusteralis yatabeana	Lamiaceae+Verbenaceae	29-33	580	0.00852	3406671	1214
8	Prenanthes tanakae	Asteraceae	28-29	20000	0.00531	2124976	108
9	Sagittaria aginashi	Alismatales	17-19	249	0.02771	11085960	49
10	Najas japonica	Najadales	17-19	205	0.02905	11618822	1782
11	Monochoria korsakowii	Pontedariaceae	22-26	34	0.03003	12010897	802
12	Iris laevigata	Iridaceae	18-18	1400	0.01574	6297533	40
13	Sparganium erectum	Sparganiaceae	22-27	20	0.03147	12588373	24
14	Sparganium japonica	Sparganiaceae	22-27	20	0.03147	12588373	139
15	Habenaria sagittifera	Orchids	17-21	20115	0.00557	2226034	3
Total							9163

has unresolved relationships between some taxa and because the tree does not include all the families of flowering plants. For details see Appendix.

The numbers of species within the upper taxa were obtained from Cronquist (1981) for the dicotyledons, from Dahlgren et al. (1985) for the monocotyledons and from Kramer and Green (1990) for the ferns and fern allies respectively. The resulting values of  $E_n[1/(m+k)]$  or  $(m+1/E_n[1/k])^{-1}$  depending on whether  $n \leq 100$  or  $n > 100$  are also presented in the sixth column of Table 2. When  $m$  is not determined uniquely, the value of  $E_n[1/(m+k)]$  or  $(m+1/E_n[1/k])^{-1}$  is calculated by using the probability of a particular value of  $m$ . For details see Appendix.

### 3.4.3 Expected Loss of Biodiversity

Let us define the unit of biodiversity as the distance on the tree of the vascular plants from any terminal nodes to the root node, and let us express the contribution of a species  $i$  to the biodiversity in terms of this unit as  $B_i$ . The values of  $B_i$  are equal to the values for  $E_n[1/(m+k)]$  or  $(m+1/E_n[1/k])^{-1}$  in Table 2. Since we assume an ultrametric tree, we may express the contribution of a species to biodiversity in terms of year on the assumption that, say, the first diversion of vascular plants occurred 400 million years ago (Margulis and Schwartz, 1988, p264; Strickberger, 1996, p289). Let  $Y_i$  represent the contribution of species  $i$  in this term, and then  $Y_i = B_i \times 4 \times 10^8$ .

Provided  $\Delta P_i$  is the increase in the reciprocal of the survival expectancy of species  $i$ , namely  $\Delta(1/T)$  for the species  $i$ , the expected loss of biodiversity (ELB) is represented by:

$$\sum_i \Delta P_i B_i$$

or

$$\sum_i \Delta P_i Y_i.$$

The values for  $\Delta P_i Y_i$  are presented in the last column of Table 2. The resulting ELB is about 9,200 years. This means Nakaikemi has a heritage of 9,200 years and this will be lost if this wetland disappears.

## **4 Benefits from the Development of Nakaikemi Wetland and Risk/Benefit Analysis**

### **4.1 Treatment of the Conservation Area**

A factor that makes the risk/benefit analysis of the development of Nakaikemi complicated is the difficulty in evaluating the conservation area with respect to ecological risk. Several threatened and rare species have been transplanted into the conservation area of 3.3 ha, and management including cultivation is being carried out in order to prevent succession.

One extreme view is to regard the nature of the wetland as perfectly conserved by this conservation area on the ground that populations of the threatened species will be maintained there. However, it is disputed on the following basis:

1. that the success of the transplant is uncertain because the ecology of aquatic plants is not well known and that three-year test is not sufficient,
2. that the introduction of insects and other animals has much more uncertainty,
3. and that the potential capacity of maintaining biodiversity must be smaller at the human-controlled conservation area of 3.3 ha than at the ecosystem on the land of 25ha unintendedly brought about as a by-product of human activities.

The other extreme view considering those points is to regard the ecosystem of Nakaikemi as being totally lost in the development in spite of the conservation area.

Depending on these two extremes, the ELB of the development of Nakaikemi would become 0 or 9,200 years. Here we will show the risk/benefit analysis can be done for both points of view.

### **4.2 Risk/Benefit Analysis: When the Conservation Area is Regarded as Maintaining the Diversity**

When the conservation area is regarded as maintaining the diversity, the ELB due to the development becomes zero. This conservation entails cost, and this cost can be regarded as the benefit loss from the conservation.

The initial investment cost for the conservation area is 1 billion yen, and its running cost is 60 million yen per year. Assuming 25 years of depreciation period and 3% of discount rate, total annual cost becomes 120 million yen.

Consequently, the benefit/risk ratio (B/R ratio) for this conservation will be 13,000 yen/year-ELB.

### **4.3 Risk/Benefit Analysis: When the Development is Regarded as Causing Loss of All the Biodiversity of the Wetland**

When the conservation area is not regarded as maintaining the diversity, then this development is regarded as bringing about some benefit at the expense of 9,200 years of ELB. The benefit from the development will be estimated as the loss in consumers' surplus and the producer's profit if the LNG plant will not be constructed, or as the increase in the cost to construct the LNG plant at another site. Theoretically the minimum of these two estimates should be regarded as the benefit from the development of Nakaikemi, and the loss in consumers' surplus and the producer's profit will become hugely larger than the cost increase for constructing at another site, so we estimated the benefit according to the latter concept.

To estimate the increase in construction cost from giving up Nakaikemi as the plant site, we assumed three alternative plans:

1. to construct the LNG plant adjacent to a new port for LNG tanker which is as far from the main consumption area as Tsuruga,
2. to construct the LNG plant at the industrial park adjacent to Fukui Port,

3. to utilize the reclaimed land, which used to be used for a coal gas plant, located at the outlet of the Yamato River (Osaka).

All these plans are thought to entail larger costs than the original plan. The first one has a disadvantage because it requires a new port for LNG tanker, while Nakaikemi is near from the existing Tsuruga Port, for which expansion is now being undertaken. In the second plan, the LNG plant becomes 75km further from the consumption area than Tsuruga, which will raise the construction cost of the pipelines. In this plan, additional investment for improving the port also becomes necessary. The third plan requires dredging for the port and the sea road, and is confronted with the difficulty in constructing pipelines in that they have to be constructed under heavily congested urban areas.

We estimated the increase in the construction cost to be 27-47 billion yen for the first plan, 91-100 billion yen for the second plan and 36-44 billion yen for the third plan. Under the assumption of a discount rate of 3% and a depreciation period of 50 years, the annual value for the cost increase ranges from 1.0 to 3.9 billion yen.

This result means that the development of Nakaikemi will bring about the benefit of 1.0-3.9 billion yen at the expense of 9,200 years of ELB. The B/R ratio is 110,000 to 420,000 yen/year-ELB.

## 5 Discussion

### 5.1 How to Use the Result

Neither the value of 9,200 years of ELB from the loss of Nakaikemi Wetland nor the B/R ratio of 13000 yen/year-ELB or 110,000-420,000 yen/year-ELB is useful when it is presented by itself. It must be compared with the corresponding values for other places, other development plans or other conservation policies. First, even just to compare ELB among several places would be useful for putting nature conservation policy on rational grounds. Secondly, comparison of the B/R ratio would lead to more cost-effective choice of conservation or development policy. If the benefit from enhancing expected biodiversity is estimated by CVM or other economic methods, then our result can be combined with it to produce 'cost-benefit analysis'.

### 5.2 Extinction in Japan and Worldwide Biodiversity

Another problem with our approach not yet discussed is the fact that we meant extinction in Japan by extinction of a species. This is due to the fact that the Red List which our calculation is based on deals with extinction in Japan, but it could be thought to reflect the notion that extinction in a country may matter because the populations of a species in the country can contribute to the biodiversity in addition to the contribution of the species as a whole. This is not consistent with our treatment of phylogenetic information, for which we assumed only a species as a whole can contribute to the diversity. However, at the present state of knowledge, it is difficult to deal with the contribution of local populations to the diversity and it is difficult to make some assumption about the state of a species in other countries while, nevertheless, biodiversity is a global matter. Taking these things into account, our treatment in this study may be the best one for the moment.

### 5.3 What Aspects of Ecological Risk are Excluded from ELB?

Our approach might give an impression as if it extremely simplified the concept of biodiversity and the values of the ecosystem. Certainly, we captured biodiversity at the species level and measured it according to the phylogenetic distance to other species. In doing so, we excluded any functional values of species in the ecosystem and for human beings. One may argue that ecological function of a species or its usefulness for human beings is more important than phylogenetic uniqueness. However, knowledge on species' ecological function or usefulness for humans is too poor to be used for weighting species. Rather, when function of species in the ecosystem is important, it should be taken into account at the stage of assessing the increments in the extinction probabilities. In fact, our assessment on the increments in the extinction probabilities is based on the simulation for the Red List, and the simulation is based on the

data about the trend of the populations in the last ten years, which are thought to reflect the functional relationships among species in the ecosystem.

We also excluded the concept of ‘ecosystem diversity’ and ‘landscape diversity’ and concentrated on ‘species diversity’ when we constructed the measure of biodiversity. One may argue that our measure would justify such a policy as to preserve particular species under human control isolatedly from the environment, or just to preserve genetic information of particular species.

We does not regard our measure of biodiversity as such a thing. It is certainly a measure of genetic diversity in the sense that it reflects phylogenetic distance between species, but we think it makes sense only when genetic information is carried by living things and the living things exist in the natural environment. Only thereby the genetic and the species diversity represents the diversity of the environment as a whole. In this sense, the species diversity is not the goal to preserve, but an indicator of the diversity of the environment as a whole, which is the ultimate object of preservation.

## Appendix: Phylogenetic Trees Used Here and Node Counting

For true ferns we assumed the tree below in Fig. 9 following Hasebe et al. (1995, p.146). The numbers of nodes above Marsileaceae, Azollaceae and Salviniaceae are 9, 10 and 10 respectively.

Osmundaceae  
 Hymenophyllaceae  
 Gleicheniaceae  
 Matoniaceae  
 Dipteridaceae  
 Schizaeaceae  
**Marsileaceae**  
**Azollaceae**  
**Salviniaceae**  
 other ferns

\*) The families including the species in Table 2 are indicated by bold letters.

Figure 9: Phylogenetic tree for true ferns

We assumed the tree in Fig. 10 for the higher taxa of seed plants following Chase et al. (1993). The numbers of the nodes above cycads and Ginkgo are 5 and 6 respectively, but the relationship among Pinaceae, other conifers and the group of Gnetales and the flowering plants is unresolved, so the number of nodes above these taxa can be 7 or 8. Let us assume the former and the latter cases can occur at the probabilities of 1/3 and 2/3 respectively. The number of nodes above the group consisting of Laurales, monocots, Magnoliales and paleoherb II may be, therefore, 11 with the probability of 1/3 and 12 with the probability of 2/3. The relationship among Laurales, monocots and {Magnoliales + paleoherb II} is also unresolved, so the number of nodes above monocots may be 12, 13 or 14. If we make the same assumption about the probabilities of the possible relationships within this group as among Pinaceae, other conifers and {Gnetales and + flowering plants}, the probabilities of the number of nodes above monocots being 12, 13 and 14 are 1/9, 4/9 and 4/9 respectively. The possible number of nodes above the taxa including the species listed in Table 2 is presented in brackets Fig 10 with their probabilities.

Within monocots we assume the tree shown in Fig. 11. *Najas japonica* in Table 1 and Table 2 belongs to Najadaceae, which is not included in the phylogenetic trees presented by Chase et al. (1993). We assume the Najadales is in the position where Potamogetonaceae is in the tree of Chase et al.. The number of nodes above Najadales is 17 with the probability of 1/9, 18 with the probability of 4/9 or 19 with the probability of 4/9.

We chose Alismatales rather than Alismataceae as the upper taxon of *Sagittaria aginashi*, because all the other families than Alismataceae in Alismatales are not included in the tree by Chase et al., which means the number of nodes above the family Alismataceae may be larger than that shown in the tree. The number of nodes above Alismatales is 17 with the probability of 1/9, 18 with the probability of 4/9 or 19 with the probability of 4/9.

There are three unresolved relationships above Iridaceae. As a result, the number of nodes above it may be 18 with the probability of 1/243, 19 with 10/243, 20 with 40/243, 21 with 80/243, 22 with 80/243 or 23 with 32/243.

cycads  
 Ginkgo  
 Pinaceae  
 other conifers  
 Gnetales  
 Ceratophyllum  
 paleoherb I  
 Laurales  
**monocots**[12( $\frac{1}{9}$ ), 13( $\frac{4}{9}$ ), 14( $\frac{4}{9}$ )]  
 Magnoliales  
 paleoherb II  
**ranunculids**[11( $\frac{1}{3}$ ), 12( $\frac{2}{3}$ )]  
 hamamelid I  
 hamamelid II  
 Gunnera  
**caryophyllids**[15( $\frac{1}{3}$ ), 16( $\frac{2}{3}$ )]  
 rosid III  
 rosid II  
**rosid I**[18( $\frac{1}{3}$ ), 19( $\frac{2}{3}$ )]  
 asterid V  
 asterid IV  
 asterid III  
**asterid II**[20( $\frac{1}{3}$ ), 21( $\frac{2}{3}$ )]  
**asterid I**[20( $\frac{1}{3}$ ), 21( $\frac{2}{3}$ )]

\*) The taxa including the species in Table 2 are indicated by bold letters.

Figure 10: Phylogenetic tree for higher taxa of seed plants

Araceae 1 (*Acorus*)  
 Araceae 2 + Lemnaceae  
**Najadales**[17( $\frac{1}{9}$ ), 18( $\frac{4}{9}$ ), 19( $\frac{4}{9}$ )]  
**Alismatales**[17( $\frac{1}{9}$ ), 18( $\frac{4}{9}$ ), 19( $\frac{4}{9}$ )]  
 Melanthiaceae 1 (*Pilea*)  
 Melanthiaceae 2 (*Aletris*)  
 Melanthiaceae 3 (*Veratrum*, *Chamaelirium*)  
 [Liliales other than Iridaceae and Orchids] + Smillacaceae  
 Velloziaceae  
 Cyclanthaceae  
 Pandanaceae  
 Taccaceae  
 Dioscoreaceae  
**commelinoids**[18( $\frac{1}{27}$ ), 19( $\frac{6}{27}$ ), 20( $\frac{12}{27}$ ), 21( $\frac{8}{27}$ )]  
 Hypoxidaceae  
 Tecophilaceae  
**Iridaceae**[18( $\frac{1}{243}$ ), 19( $\frac{10}{243}$ ), 20( $\frac{40}{243}$ ), 21( $\frac{80}{243}$ ), 22( $\frac{80}{243}$ ), 23( $\frac{32}{243}$ )]  
 Asparagales other than Tecophilaceae and Hyposidaceae  
**Orchids**[17( $\frac{1}{81}$ ), 18( $\frac{8}{81}$ ), 19( $\frac{24}{81}$ ), 20( $\frac{32}{81}$ ), 21( $\frac{16}{81}$ )]

\*) The taxa including the species in Table 2 are indicated by bold letters.

Figure 11: Phylogenetic tree for monocots



There are two unresolved relationships above Orchids. Accordingly, the number of nodes above it may be 17 with the probability of  $1/81$ , 18 with  $8/81$ , 19 with  $24/81$ , 20 with  $32/81$  or 21 with  $16/81$ . Three families are included in Orchids. We chose this higher taxon than the family Orchidaceae because the number of nodes above Orchidaceae, which includes *Habenaria sagittifera*, may be larger than that shown in the original tree of Chase et al. due to the lack of the other two families in the tree.

There is an unresolved relationship above commelinoids. As a result, the number of nodes above this taxon may be 18 with the probability of  $1/27$ , 19 with  $6/27$ , 20 with  $12/27$  or 21 with  $8/27$ . The tree within commelinoids is presented in Fig. 12.

Araceae  
 Zingiberales  
 Haemodoraceae  
 Philydraceae  
**Pontederiaceae** [ $22(\frac{1}{81})$ ,  $23(\frac{8}{81})$ ,  $24(\frac{24}{81})$ ,  $25(\frac{32}{81})$ ,  $26(\frac{16}{81})$ ]  
 Commelinaceae  
 Bromeliaceae  
 Rapateaceae  
 Typhaceae  
**Sparganiaceae** [ $22(\frac{1}{243})$ ,  $23(\frac{10}{243})$ ,  $24(\frac{40}{243})$ ,  $25(\frac{80}{243})$ ,  $26(\frac{80}{243})$ ,  $27(\frac{32}{243})$ ]  
 Cyperales  
 Poales + Eriocaulaceae

\*) The taxa including the species in Table 2 are indicated by bold letters.

Figure 12: Phylogenetic tree for commelinoids

There is one unresolved relationship above Pontederiaceae and two unresolved relationships above Sparganiaceae. The resulting possible numbers of nodes for them are presented in brackets in Fig. 12 with their probabilities.

There are 38 families that are not included in the tree of Chase et al. other than the four families in Alismatales, seven in Najadales and two in Orchids mentioned above. We assumed addition of these families does not affect the number of nodes above the chosen upper taxa for the species listed in Table 2, i.e., these not included families make a monophyletic clades with their adjacent families.

For caryophyllids, rosid I, asterid II and asterid I the inner phylogenetic trees are presented in Figs. 13, 14, 15 and 16 respectively. The possible numbers above the upper taxa for the species listed in Table 2 are presented in brackets with their probabilities. Why those numbers are possible is explained in the notes to the figures.

Santalales  
 Droseraceae  
 Nepentaceae  
**Polygonaceae** [ $20(\frac{1}{3})$ ,  $21(\frac{2}{3})$ ]  
 Plumbaginaceae  
 Caryophyllales

\*) The taxa including the species in Table 2 are indicated by bold letters.

Figure 13: Phylogenetic tree for caryophyllids

Geraniaceae  
 Saxifragaceae  
 Greyiaceae  
 Combretaceae  
 Melastomataceae  
 Vochysiaceae  
 Myrtaceae  
 Punicaceae  
**Trapaceae** [25( $\frac{5}{51}$ ), 26( $\frac{15}{51}$ ), 27( $\frac{14}{51}$ ), 28( $\frac{11}{51}$ ), 29( $\frac{6}{51}$ )]  
 Lythraceae  
 Onagraceae  
 Oxalidaceae  
 Eucryphiaceae  
 Cunoniaceae  
 Tremandraceae  
 Cephalotaceae  
 other rosid I

\*) The taxa including the species in Table 2 are indicated by bold letters. The number of nodes above Trapaceae was determined taking into account the possibility that Penaeaceae, Crypteromiaceae and Thymelaeaceae, which are not included in the tree by Chase et al. (1993), make a clade with Trapaceae.

Figure 14: Phylogenetic tree for rosid I

Aquifoliaceae  
 Grossulariaceae 1 (*Phyllonoma*)  
 Cornaceae 1 (*Helwingia*)  
 Grossulariaceae 2 (*Escallonia*)  
 Campanulaceae  
 Menyanthaceae 1 (*Menyanthes*)  
 Menyanthaceae 2 (*Villarsia*)  
 Cornaceae 2 (*Corokia*)  
**Asteraceae** [28( $\frac{1}{3}$ ), 29( $\frac{2}{3}$ )]  
 Goodeniaceae  
 Calyceraceae  
 other asterid II

\*) The taxa including the species in Table 2 are indicated by bold letters.

Figure 15: Phylogenetic tree for asterid II

Eucommiaceae  
 Garryaceae  
 Cornaceae  
 Loganiaceae 1 (*Gelsemium*)  
 Loganiaceae 2 (*Spigelia*)  
 Asclepiadaceae  
 Apocynaceae  
 Rubiaceae  
 Gentianaceae  
 Saxifragaceae  
 Oleaceae  
 Byblidaceae  
 Bignoniaceae  
 Buddlejaceae  
 Pedaliaceae 1 (*Proboscidea*)  
 Pedaliaceae 2 (*Harpogophytum*)  
 Pedaliaceae 3 (*Sesamum*)  
**Lamiaceae + Verbenaceae** [29( $\frac{1}{46}$ ), 30( $\frac{7}{46}$ ), 31( $\frac{14}{46}$ ), 32( $\frac{16}{46}$ ), 33( $\frac{8}{46}$ )]  
 other Scrophulariales  
 other asterid I

\*) The taxa including the species in Table 2 are indicated by bold letters. We chose Lamiaceae + Verbenaceae as the upper taxon for *Eusteralis yatabeana* rather than Lamiaceae because they are not monophyletic in the tree by Chase et al. (1993). The number of nodes above Lamiaceae + Verbenaceae was determined taking into account the existence of two unresolved relationships above it and the possibility that Lennoaceae, which is not included in the tree by Chase et al. (1993), makes a clade with Lamiaceae + Verbenaceae.

Figure 16: Phylogenetic tree for asterid I

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