



# Article Spatial Evaluation of Greenhouse Gas Fluxes in a Sasa (Dwarf Bamboo) Invaded Wetland Ecosystem in Central Hokkaido, Japan

Akane Kagemoto<sup>1</sup>, Fumiaki Takakai<sup>1,2,\*</sup>, Osamu Nagata<sup>3</sup>, Masayuki Takada<sup>4,5</sup> and Ryusuke Hatano<sup>6</sup>

- <sup>1</sup> Graduate School of Agriculture, Hokkaido University, Hokkaido 060-8589, Japan; ak.SSLHU@gmail.com
- <sup>2</sup> Faculty of Bioresource Sciences, Akita Prefectural University, Akita 010-0195, Japan
- <sup>3</sup> Hokkaido Agricultural Research Center, National Agriculture and Food Research Organization, Hokkaido 062-8555, Japan; nagaosa@affrc.go.jp
- <sup>4</sup> Hokkaido Institute of Environmental Sciences, Hokkaido 060-0819, Japan; mtakada@hosei.ac.jp
- <sup>5</sup> Faculty of Sustainability Studies, Hosei University, Tokyo 102-8160, Japan
- <sup>6</sup> Research Faculty of Agriculture, Hokkaido University, Hokkaido 060-8589, Japan;
  - hatano@chem.agr.hokudai.ac.jp
- Correspondence: takakai@akita-pu.ac.jp

**Abstract:** To evaluate the effect of vegetation change on greenhouse gas (GHG) budget from a wetland ecosystem, the CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O budgets from whole area (21.5 ha) of the Bibai Wetland, where dwarf bamboo (*Sasa*) or *Ilex* has invaded into original *Sphagnum* dominated vegetation, located in Hokkaido, Japan were estimated. The original *Sphagnum*-dominated vegetation was changed from a sink to a source of CO<sub>2</sub> by invasion of short-*Sasa* (50 cm > height), while the invasion of tall-*Sasa* (50 cm < height < 150 cm) or *Ilex* increased CO<sub>2</sub> uptake. Annual CH<sub>4</sub> emission was decreased by the invasion of *Sasa* or *Ilex*. The annual N<sub>2</sub>O emission was slightly increased by invasion of *Ilex* only. These GHG budgets were correlated with the environmental factors related to the water table depth. The distribution of vegetation and environmental factors was estimated from satellite image bands, and the GHG budget of the entire wetland was estimated. The whole wetland area was considered to be a sink for GHG (-113 Mg CO<sub>2</sub>-eq y<sup>-1</sup>) and CO<sub>2</sub> uptake by tall-*Sasa* occupied 71% of the GHG budget. The vegetation change due to the lowering of the water table depth currently increases the rate of carbon accumulation in the ecosystem by about 5 times.

Keywords: closed chamber method; greenhouse gas; satellite image analysis; vegetation change

# 1. Introduction

The area of peat-forming wetlands is estimated to be 230–250 Mha globally [1,2], which is about 1.5% of the total terrestrial area. Wetland ecosystems in their natural state generally accumulate large amounts of carbon (C) in the form of peat over long periods of time, as plant production exceeds organic matter decomposition due to their wet environment [3]. The amount of carbon stored in northern peatlands is estimated to be 450 Pg (petagram,  $10^{15}$  g), which is one third of the global soil C storage [1]. While peatlands absorb carbon dioxide (CO<sub>2</sub>) and play an important role as a sink for C, they also produce and emit methane (CH<sub>4</sub>) through the anaerobic decomposition of organic matter. CH<sub>4</sub> emission from natural wetlands are considered to be an important source of CH<sub>4</sub> [4]. The release of nitrous oxide (N<sub>2</sub>O) has been shown to be small in wetlands under natural conditions, but can be a large source when subjected to anthropogenic drainage and drying [5].

Greenhouse gas (GHG) fluxes from wetlands are highly spatio-temporally variable and are influenced by a variety of factors, including environmental factors such as air and soil temperature, moisture condition, and solar radiation, as well as soil chemical properties and vegetation. The net ecosystem exchange of  $CO_2$  (NEE) in wetlands is determined by the balance between  $CO_2$  uptake by photosynthesis and  $CO_2$  emission from plant and soil respiration. Although wetland ecosystems exhibit  $CO_2$  uptake in the



Citation: Kagemoto, A.; Takakai, F.; Nagata, O.; Takada, M.; Hatano, R. Spatial Evaluation of Greenhouse Gas Fluxes in a *Sasa* (Dwarf Bamboo) Invaded Wetland Ecosystem in Central Hokkaido, Japan. *Atmosphere* **2021**, *12*, 448. https://doi.org/ 10.3390/atmos12040448

Academic Editors: Jianghua Wu, Gareth Marshall, Meng Wang, Qiu'an Zhu and Mei Wang

Received: 14 March 2021 Accepted: 30 March 2021 Published: 31 March 2021

**Publisher's Note:** MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Copyright:** © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). long-term, fluctuations in photosynthesis and respiration can cause interannual variability in NEE over a considerable range from uptake to release [6]. Instantaneous values of photosynthesis are generally related to photosynthetically available radiation (PAR), while respiration is related to temperature (soil and air temperature) [7,8]. Spatial variations in annual NEE values have been explained by differences in vegetation, groundwater level, and plant biomass [7,9]. CH<sub>4</sub> fluxes from wetlands have been measured mainly in northern peatlands and reported to have large spatio-temporal variability. Temporal variations of CH<sub>4</sub> fluxes are due to air temperature [10], soil temperature, groundwater level, and atmospheric pressure [11]. Spatial variations in CH<sub>4</sub> fluxes have been reported to occur due to differences in groundwater level [12,13], plant biomass and vegetation characteristics [14], temperature and topography [15]. Spatio-temporal variations in N<sub>2</sub>O have been reported to be due to lowering of the groundwater table [16–19], but there are few examples of measurements and the details are unknown.

Scaling up plot-level GHG flux measurements to regional and global scales is important for understanding the interaction between climate change and GHG emissions from wetlands. However, scaling up GHG fluxes from wetlands with large spatio-temporal variability is challenging. As a method to evaluate GHG emissions from wetlands over a wide area, classifications of wetland components (topography and vegetation) and estimation of area cover using satellite images have been used. A combination of land surface classification using Landsat satellite imagery and flux measurements has been used to estimate basin-level  $CO_2$  and  $CH_4$  budgets in the tundra of northeastern Europe in Russia [20] and landscape-level CH4 budgets in the wetland-upland complex ecosystem of Canada [21] estimates have been reported.

Wetland ecosystems are based on a delicate balance of environmental factors such as moisture conditions, and are considered to be sensitive to environmental changes. In addition to indirect effects such as climate change, wetland environments are also greatly affected by direct anthropogenic disturbances such as drainage for agricultural use. The anaerobic peat soils in wetlands rapidly become aerobic when drained. This results in increased CO<sub>2</sub> emission due to accelerated organic matter decomposition [22], decreased CH<sub>4</sub> emission [17,18], and depending on the type of wetland, increased N<sub>2</sub>O emission [17–19].

About 80% of Japan's peatlands are distributed in the Hokkaido region (about 200,000 ha), a northern part of Japan with a cool climate. It is thought that almost all this peatland was originally a wetland, but most of it has disappeared by now due to agricultural development since 1870. The area of Ishikari Mire Complex, the largest in Hokkaido, which used to be spread out in the Ishikari River basin, has decreased to 0.2% in 1983 (119 ha) compared to 1870 (50,690 ha) [23]. Even in wetlands that have avoided disappearance due to agricultural development, changes in the wetland environment have occurred due to indirect effects of development. Typical examples are the influx of sediment into the wetland (floodplain mire) and following expansion of alder (*Alnus japonica*) forests due to human activities around the wetland [24,25], and the drying of the wetland and following invasion of *Sasa* (dwarf bamboo) [26–28]. These changes in the wetland environment may alter its GHG budget.

In this study, to assess the impact of vegetation change triggered by drainage due to agricultural land development on the GHG budget of wetland ecosystems, we conducted a spatial estimation of GHG fluxes in a *Sasa* invaded wetland ecosystem.

#### 2. Materials and Methods

# 2.1. Study Site

This study was conducted at the Bibai Wetland (43°19′N, 141°48′E), located in Ishikari peatland, central Hokkaido, northern part of Japan (Figure 1). In the surrounding area of Bibai Wetland, most of the wetlands have been disappeared due to agricultural reclamation since 1870. At present, about 22 ha of the Bibi wetland is preserved, but it is surrounded by agricultural land and related open ditches on all sides, and it has been pointed out that the wetland is drying up [29]. In the central part of the wetland, where we conducted

this survey, 3.5 to 4.5 m of peat accumulated on the mineral soil (Figure 2). In the peat profile, low moor peat, (minerotrophic fen type), transitional peat and high moor peat (ombrotrophic bog type) are deposited in order from the bottom [30]. The high moor peat consisting of undecomposed residues of peat moss (*Sphagnum* spp.), sedges (*Carex* spp.), and vines (*Vaccinium oxycoccus*), is deposited at nearly 2 m. The peat at a depth of 10–30 cm has a high ash content and low T-C content due to the contamination of volcanic tephra that erupted nearly 300 years ago [30].





The original vegetation of the wetland was mainly sphagnum moss (*Sphagnum*) and sedge plants, which covered the entire wetland in the early 1960s [29], but as the wetland became drier, dwarf bamboo (*Sasa*) invaded from the surrounding areas. The current vegetation consists of about 1 ha of *Sphagnum papillosum*, *Moliniopsis japonica*, *Carex mid-dendorffii*, and *Eriophorum vaginatum* in the center of the wetland. Surrounding the *Sphagnum*-dominated vegetation, there is a vegetation of mainly *Sasa palmata* and *Gale belgica* var. tomentosa. *Rhus trichocarpa* is found in the more dried eastern part of the wetland, and *llex crenata* var. paludosa in the southwestern part of the wetland (Figure S1). The mean annual temperature at this region is 7.1 °C and the mean annual precipitation is 1156 mm. The snow season is usually from mid-November to mid-April.

# 2.2. Fluxes of CO<sub>2</sub> (Net Ecosystem Exchange of CO<sub>2</sub>: NEE), CH<sub>4</sub> and N<sub>2</sub>O

This study was conducted from January 2004 to November 2006. GHG flux measurement plots were set up from the area of *Sphagnum-Moliniopsis* vegetation in the central part of the wetland to the area dominated by *Sasa* and *Ilex* (Figure 1). Corresponding to the vegetation change, three to seven measurement plots were established in the *Sphagnum-Moliniopsis* site (hereafter "*Sphagnum* site"), the short-*Sasa* site (height of *Sasa* < 50 cm), the tall-*Sasa* site (50 cm < height of *Sasa* < 130 cm), and the *Ilex* site (from June 2005), respectively (Figure 1 and Figure S1). The measurement plots were changed in June 2005 within each vegetation site.



**Figure 2.** Peat C and N content (**a**,**b**), C/N ratio (**c**), and ash content (**d**) by depth in the Bibai wetland. The high ash content and low T-C content of the peat at a depth of 10–30 cm is due to the contamination of volcanic tephra.

GHG (CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O) fluxes from ecosystems were measured using a closed chamber method. In order to measure the emission and absorption of GHG by vegetation, a transparent acrylic chamber ( $30 \times 30$  cm (small chamber) or  $60 \times 60$  cm (large chamber) at the bottom, 50–130 cm high depending on the vegetation) was used and left the vegetation inside the chamber during the measurement [31–34]. For small chambers, chamber collars ( $30 \times 30$  cm at the bottom) equipped with a groove on the top were inserted into the peat surface to a depth of 5 cm before the beginning of this study. The groove was filled with water, and the chamber was inserted into the groove during each gas flux measurement. For large chambers, the transparent acryl chamber consisted of a rectangular main body ( $60 \times 60$  cm at the bottom, 50–130 cm in height) equipped with a groove on the top, and a detachable lid was used. The main bodies were inserted into the peat surface to a depth of 5 cm before the beginned in place throughout the measurement period. As well as the small chamber, the groove of the large chamber was filled with water, and the lid was inserted into the groove during each gas flux measurement period. As well as the small chamber, the groove of the large chamber was filled with water, and the lid was inserted into the groove during each gas flux measurement. Boardwalks were set up near the measurement plots to prevent disturbance during the measurement.

GHG fluxes were measured at 0 and 4 min after sealing the chamber for  $CO_2$  (net ecosystem exchange of  $CO_2$ : NEE), 0, 10 and 20 min for  $CH_4$  and 0 and 20 min for  $N_2O$ , respectively. Gas samples were collected in Tedlar bags ( $CO_2$ ) and vacuum vials ( $CH_4$  and  $N_2O$ ) and brought back to the laboratory for analysis. The frequency of surveys was 2–4 times per month during the growing season (non-snow season) and about once every month or two during the snow season. GHG fluxes from the snow surface were measured during the snow season. Simultaneously with the GHG flux measurements, soil temperature at a depth of 3 cm, water table depth, and photosynthetically active radiation (PAR) by a photon sensor (PAR-01, PREDE, Tokyo, Japan) were measured.

The concentration of CO<sub>2</sub> was analyzed using an infrared gas analyzer (ZFP5 or ZFP9, Fuji Electric, Tokyo, Japan), and CH<sub>4</sub> and N<sub>2</sub>O were analyzed using a gas chromatograph equipped with a flame ionization detector and an electron capture detector, respectively (GC-8A and GC-14B, respectively, Shimadzu, Kyoto, Japan). The GHG fluxes were calcu-

lated by linear regression of the measurement time and the change in GHG concentration in the chamber. Positive and negative values of GHG fluxes indicate the net emission from the ecosystem to the atmosphere and the net uptake from the atmosphere to the ecosystem, respectively.

#### 2.3. Total Ecosystem Respiration and Gross Photosynthesis

Net ecosystem exchange of  $CO_2$ , i.e.,  $CO_2$  fluxes from the whole ecosystem (plant and soil), consisted of  $CO_2$  emission by respiration of the whole ecosystem and  $CO_2$  uptake by photosynthesis. Therefore, the relationship is described as Equation (1):

$$NEE = R_{TOT} - P_G \tag{1}$$

where  $R_{\text{TOT}}$  is the total ecosystem respiration, and  $P_{\text{G}}$  is the gross photosynthetic CO<sub>2</sub> uptake. In terms of NEE, CO<sub>2</sub> uptake is a negative value and CO<sub>2</sub> emission to the atmosphere is a positive value. In the equation, both  $R_{\text{TOT}}$  and  $P_{\text{G}}$  are presented by absolute values. After the measurement of NEE by the transparent chamber, the  $R_{\text{TOT}}$  was immediately measured under light shielding condition (100% shading) with an opaque cover.  $P_{\text{G}}$  was estimated by subtracting NEE by  $R_{\text{TOT}}$  according to Equation (1).

To establish a PAR- $P_G$  curve, shading nets (60, 70, and 90% shading) were placed over the transparent chambers, and NEE measurements at low PAR level were also performed about once a month during the growing season. A photon sensor was installed at 120 cm above the ground in the center of the wetland and the PAR was continuously measured at 5-min intervals using a data logger (F-80, M.C.S., Sapporo, Japan). The soil temperature (3 cm) of each vegetation site was also measured continuously at 1-h intervals using a data logger.

# 2.4. Calculation of Cumulative GHG budgets

To calculate the cumulative NEE value during the growing season, estimation curve of  $T_{3cm}$  (soil temperature at a depth of 3 cm)- $R_{TOT}$  and PAR- $P_{G}$  were established at each measurement plots:

$$R_{\rm TOT} = a \times e^{b \times T3\rm cm} \tag{2}$$

where  $T_{3 \text{ cm}}$  is the soil temperature at a depth of 3 cm, *a* and *b* are regression constants.

A PAR-  $P_{\rm G}$  curve is generally expressed by the following Equation (3) (e.g., [7]):

$$P_{\rm G} = (Q \times {\rm PAR})/(K + {\rm PAR}) \tag{3}$$

where *Q* is the maximum  $P_G$  under light-saturated conditions, *K* is the light intensity at which 50% of the maximum  $P_G$  and *a* and *b* are regression constants. In order to account for seasonal changes in the curve, *Q* was assumed to vary linearly with the variation of the average temperature for two weeks before and after the measurement date (totally about one month), and was converted to " $Q = c \times$  (average temperature for one month), where c is a constant". This gives Equation (4) as follows:

$$P_{\rm G} = (c \times (\text{average temperature for one month}) \times \text{PAR})/(K + \text{PAR})$$
 (4)

Using Equation (4), *c* and *K* were determined by non-linear regression (Kaleida graph, Synergy Softare). The *c* and *K* were calculated for each plot, and since the number of low PAR measurements was not sufficient for some of the short-*Sasa* and tall-*Sasa* plots, the average of constant *K* for other plots in the same vegetation site was used to create the equation.

Using the continuous values of soil temperature (3 cm) and PAR, continuous values of  $R_{\text{TOT}}$  and  $P_{\text{G}}$  at 1-h intervals were calculated from Equations (2) and (4), respectively. NEE was then calculated using Equation (1) and integrated over the growing season. NEE during the snow season and the cumulative values of CH<sub>4</sub> and N<sub>2</sub>O were calculated by a linear interpolation. The cumulative period of GHG budget was two years, from January to December in 2004 and from June 2005 to June 2006, and the averaged value was

indicated as the annual GHG budget of each plot. The net GHG budget was calculated by multiplying the annual budgets of  $CO_2$ ,  $CH_4$ , and  $N_2O$  by the global warming potential (GWP,  $CO_2$ : $CH_4$ : $N_2O = 1:34:298$ ) [4], which takes radiative forcing into account.

# 2.5. Physico-Chemical Properties of Peat and Dissolved Organic Carbon (DOC) Concentration of Groundwater at the Flux Measurement Plots

In August 2006, bulk peat samples were collected from the surface layer of 0–10 cm at GHG flux measurement plots (20 plots in total). The samples were dried at 105 °C for 48 h to determine the moisture content. A part of the samples was air-dried and then ground for analysis. The degree of humification of the peat was determined according to Kaila's method [35,36], and the total carbon and nitrogen contents (T-C and T-N, respectively) were measured with an N/C analyzer (SUMIGRAPH NC-1000, Sumika Chemical Analysis Service, Osaka, Japan).

As with the peat samples, a stainless-steel tube was inserted into the peat at the flux measurement plots and groundwater was collected at a depth of 50 cm. The dissolved organic carbon (DOC) concentration of the groundwater was measured using a TOC Analyzer (SHIMADZU TOC-5000A, Shimadzu, Kyoto, Japan).

#### 2.6. Observing the Spatial Distributions of Vegetation and Environmental Factors

Grid points were set at  $50 \times 50$  m intervals on the southern half of the wetland (Figure 1), and latitude and longitude were measured using GPS. In July 2006, the vegetation coverage within a radius of about 15 m from the grid points was recorded and classified into five vegetation communities: *Sphagnum-Moliniopsis, Moliniopsis-Gale, Sasa, Sasa-Gale, Ilex. Sasa* height (8 replicates at each point) and water table depth were measured 5 times between September 2005 and September 2006 and averaged. Peat and groundwater were also collected and analyzed in August 2006 from the grid points as well as the gas flux measurement plots indicated in Section 2.5., except for peat C and N contents.

#### 2.7. Estimating the Distributions of Vegetation and Environmental Factors Using Satellite Imagery

#### 2.7.1. Satellite Imagery

The IKONOS image taken in September 2002 was used in this study. The ground resolution of IKONOS is 4 m. The four bands obtained by the satellite are Band 1, blue (445–516 nm); Band 2, green (506–595 nm); Band 3, red (632–698 nm); Band 4, near infrared (757–853 nm). The pixel values of the bands at each studied plot (grid points and GHG flux measurement plots) were obtained. Normalized vegetation index (NDVI) and ratio vegetation index (RVI) as vegetation indices indicating the amount and vigor of plants were obtained from the following Equations (5) and (6)

$$NDVI = (Band 4 - Band 3)/(Band 4 + Band 3)$$
(5)

$$RVI = (Band 4/Band 3)$$
 (6)

#### 2.7.2. Estimating the Distribution of Vegetation

Using the vegetation classification surveyed at all plots as the objective variable and the satellite pixel values (Band 1–4, NDVI and RVI) as explanatory variables, discriminant analysis was conducted on all combinations of explanatory factors. Vegetation discrimination using Mahalanobis' distance was conducted for the combinations of factors with the highest discriminant validity (Band 1, 2, and 4). The accuracy rate (the ratio of the number of correctly discriminated samples to the number of samples used in the discriminant analysis) was calculated for each vegetation community and for the entire vegetation. Using the *Sasa* and *Sasa-Gale* communities as the *Sasa* site, the *Sphagnum-Moliniopsis* and *Moliniopsis-Gale* communities as the *Sphagnum* site, and the *Ilex* community as the *Ilex* site, the area of each vegetation site was calculated.

#### 2.7.3. Estimating the Distributions of Environmental Factors

Multiple regression was performed with environmental factors as the objective variable and satellite pixel values (Band 1–4, NDVI and RVI) as the explanatory variables. The obtained regression equation was used to estimate the distribution of *Sasa* height and environmental factors in the entire wetland. The estimation of *Sasa* height was conducted in the *Sasa* site (*Sasa* and *Sasa-Gale* communities). The water table depth, moisture content of surface peat and DOC concentration of groundwater were estimated by multiple regression for the *Sphagnum*, *Sasa* and *Ilex* sites, respectively. Multiple regression was performed using 80% of the total data. Since a multiple regression was not able to be conducted for the *Ilex* site due to the small number of plots, a single regression was conducted and the factor with the highest regression coefficient was selected.

#### 2.7.4. Verification of Estimation Accuracy

In order to verify the accuracy of the vegetation classification and *Sasa* height, a field survey was conducted in September 2006 at different plots from the grid points. The vegetation classification was verified at 26 sites, and the accuracy rate of the classification was calculated. *Sasa* height was verified at 12 sites, and the measured values were compared with the estimated values. For the water table depth, moisture content of the surface peat, and groundwater DOC, the remaining 20% of the data that were not used for multiple regression were used to compare the measured and estimated values.

#### 2.8. Statistical Analysis

Statistical analyses were performed using Excel statistics 2012 for Windows (SSRI, Tokyo, Japan). Differences in the environmental factors, GHG budgets and bands among the vegetation sites were compared using a Tukey's HSD test (p < 0.05).

#### 3. Results

#### 3.1. Spatio-Temporal Variation of GHG Fluxes

Seasonal variations of environmental factors and GHG fluxes during the measurement period are shown in Figure 3 and Figure S2.

The soil temperature (3 cm) in the tall-*Sasa* and *Ilex* sites were relatively lower compared to that in the *Sphagnum* site. During periods of low precipitation, the water table depth in the *Ilex* site was lower than in the other sites, with a maximum drop of nearly 50 cm.

The daytime NEE in the *Sphagnum* and *llex* sites showed an uptake of CO<sub>2</sub> throughout the growing season, and the uptake increased during the summer. Daytime NEE in the short- and tall-*Sasa* sites showed emission of CO<sub>2</sub> just after the snow melting, thereafter, tended to uptake CO<sub>2</sub> from the beginning of July. The NEE in the tall-*Sasa* site tended to show greater absorption of CO<sub>2</sub> than that in the short-*Sasa* site. The NEE in the *llex* site tended to be absorbed CO<sub>2</sub> throughout the growing season and remained higher absorption than that of other vegetation site. Large CO<sub>2</sub> uptake was found just before the snow season in the tall-*Sasa* and *llex* sites. The CH<sub>4</sub> flux in the *Sphagnum* site tended to show emission throughout the growing season, and tended to increase in the summer. Though the CH<sub>4</sub> fluxes in the short- and tall-*Sasa* sites remained at a lower level compared to that in the *Sphagnum* site, sometimes episodic high CH<sub>4</sub> emissions were found. The CH<sub>4</sub> fluxes in the *llex* site varied between slight emission and uptake. The N<sub>2</sub>O fluxes in the studied wetland varied between slight emission and uptake, except for slightly higher emission from the *llex* site. During the snow season, there was little emission or uptake of any GHG in all vegetation sites.



**Figure 3.** Seasonal changes in daily air temperature, precipitation and snow depth ((a) line, black and grey bars, respectively), soil temperature at 3 cm depth (b), water table depth (c), Net Ecosystem Exchange (NEE) (d) and  $CH_4$  (e) and  $N_2O$  (f) fluxes. Error bars indicate minimum and maximum value. Positive fluxes indicate net emissions to the atmosphere and negative fluxes indicate net uptake from the atmosphere.

 $R_{\text{TOT}}$  were significantly positively correlated with soil temperature (3 cm) and water table depth in all vegetation sites (Table S1). The CH<sub>4</sub> fluxes were significantly positively correlated with soil temperature (3 cm) in the *Sphagnum* and short-*Sasa* sites. There was also a significant positive correlation between CH<sub>4</sub> flux and water table depth in the *Sphagnum* site. The temporal variation in CH<sub>4</sub> fluxes in the tall-*Sasa* and *Ilex* sites could not be explained by soil temperature (3 cm) and water table depth. N<sub>2</sub>O fluxes were not significantly correlated with soil temperature of (3 cm) and water table depth in all vegetation sites.

#### 3.2. Estimating Cumulative NEE

There were significant exponential correlations between the soil temperature (3 cm) and  $R_{\text{TOT}}$ , and significant regression expressions with  $R^2 = 0.673$  to 0.941 (p < 0.05) were obtained in all plots (Table S2 and Figure S3). Based on the regression of the  $P_G$  with PAR and the average monthly temperature, significant estimation curves for 11 of the 23 plots were established (Table S2). For the plots where estimation curves could not be established, the constant *K* was set to the average value of the same vegetation site, and the constant *c* was determined to establish the estimation curve. The correlation coefficients (*R*) of the estimation curves for  $P_G$  in the *Sphagnum* site ranged from 0.373 to 0.877 (Table S2), and the curves corresponded relatively well to the measured values compared to other vegetation sites (Figure S4). High  $P_G$  were sometimes measured at low PAR in the *Ilex* site, and some plots deviated from the estimation curves.

# 3.3. Annual GHG Budgets

The annual GHG budgets in each site are shown in Table 1. The  $R_{\text{TOT}}$  in the *llex* site was significantly higher than those in the other three sites. The  $P_{\text{G}}$  in the *Sphagnum* and short-*Sasa* sites were similar, and the  $P_{\text{G}}$  in the tall-*Sasa* and *llex* sites were significantly higher than those in the other two sites. The annual NEE of the *Sphagnum* and short-*Sasa* sites were negative and positive ( $-49.7 \pm 40.2$  and  $124 \pm 42.9$  g C m<sup>-2</sup> y<sup>-1</sup>, respectively), indicating net CO<sub>2</sub> uptake and emission, respectively. The annual NEE of the tall-*Sasa* and *llex* sites showed higher CO<sub>2</sub> uptake ( $-240 \pm 79.5$  and  $-990 \pm 90.9$  g C m<sup>-2</sup> y<sup>-1</sup>, respectively) than that of the *Sphagnum* site, and the annual NEE of the *llex* site was significantly different from those of the other three sites.

**Table 1.** Greenhouse gas (GHG) budgets at each vegetation site.

| Site   | Sphagnum                   | Short-Sasa                | Tall-Sasa                | Ilex                    |
|--|----------------------------|---------------------------|--------------------------|-------------------------|
| $R_{\rm TOT} ({\rm g}{\rm C}{\rm m}^{-2}{\rm y}^{-1})$               | $494\pm39~\mathrm{a}$      | $594\pm117~\mathrm{a}$    | $815\pm119~\mathrm{a}$   | $1713\pm127~\mathrm{b}$ |
| $P_{\rm G} ({\rm g}{\rm C}{\rm m}^{-2}{\rm y}^{-1})$                 | $544\pm18$ a               | $470\pm76$ a              | $1055\pm178~\mathrm{b}$  | $2702\pm148~{\rm c}$    |
| NEE (g C m <sup><math>-2</math></sup> y <sup><math>-1</math></sup> ) | $-49.7\pm40.2~\mathrm{bc}$ | $124\pm43~{ m c}$         | $-240\pm80\mathrm{b}$    | $-990\pm91$ a           |
| $CH_4$ (g C m <sup>-2</sup> y <sup>-1</sup> )                        | $11.2\pm1.9\mathrm{b}$     | $6.91\pm2.52~\mathrm{ab}$ | $3.42\pm1.23~\mathrm{a}$ | $0.169 \pm 0.166$ a     |
| $N_2O (mg N m^{-2} y^{-1})$  | $5.05\pm4.02~\mathrm{a}$   | $4.37\pm3.91$ a           | $-4.54\pm9.24$ a         | $47.2\pm9.5~\mathrm{b}$ |
| Net GHG $(g \operatorname{CO}_2 \operatorname{-eq} m^{-2} y^{-1})$   | $326\pm203~{\rm c}$        | $771\pm130~{\rm c}$       | $-728\pm302$ b           | $-3599 \pm 335$ a       |

NEE, net ecosystem exchange of CO<sub>2</sub>;  $P_G$ : gross photosynthesis;  $R_{TOT}$ : total ecosystem respiration. Both  $R_{TOT}$  and  $P_G$  are presented by absolute values. For NEE, CH<sub>4</sub> and N<sub>2</sub>O, positive values indicate net emissions to the atmosphere and negative values indicate net uptake from the atmosphere. Numbers represent the average  $\pm$  standard error. Numbers within a line followed by different letters differ significantly among the sites. (p < 0.05, Tukey-Kramer test).

The annual CH<sub>4</sub> emission was lower in the order of the *Sphagnum* > short-*Sasa* > tall-*Sasa* > *Ilex* sites, and was significantly lower in the tall-*Sasa* and *Ilex* sites than in the *Sphagnum* site. The annual N<sub>2</sub>O emission from the *Ilex* site was significantly higher than that in the other three sites.

The net GHG budget in each vegetation site was positive (emission) in the *Sphagnum* and short-*Sasa* sites, but negative (uptake) in the tall-*Sasa* and *Ilex* sites. The N<sub>2</sub>O emissions accounted for only a small percentage of net GHG budget in all sites (<1%). In absolute values,  $CO_2$  and  $CH_4$  accounted for 34.6 and 65.0% of the net GHG budget in the Sphagnum site, 68.1 and 31.6% in the short-*Sasa* site, 89.2 and 10.6% in the tall-*Sasa* site, and 99.3 and 0.142% in the *Ilex* site, respectively. The contribution of  $CO_2$  to the net GHG budget was larger at the sites invaded by *Sasa* and *Ilex*.

#### 3.4. Relationships between Annual GHG Budgets and Environmental Factors

The physico-chemical properties of surface peat and groundwater DOC concentrations at the flux measurement plots are shown in Table 2. The moisture content in the *llex* site was significantly lower than that in the other three sites. Kaila's degree of humification, which is used as an indicator of peat decomposition, was significantly lower in the *Sphagnum* site than in the other three sites. The T-C and T-N contents and C/N ratio of peat in the *llex* site tended to be lower than those in the other three sites. Although there was no significant difference, the groundwater DOC concentration in the *Sphagnum* site tended to be lower than those in the other three sites.

**Table 2.** Physico-chemical properties of surface peat layer (0–10 cm) and ground water dissolved organic carbon (DOC) at flux measurement plots.

|   | Sphagnum                 | Short-Sasa               | Tall-Sasa                | Ilex                     |
|---|--------------------------|--------------------------|--------------------------|--------------------------|
| Moisture content (%)                        | $90.4\pm0.8\mathrm{b}$   | $88.4\pm0.8~{ m b}$      | $88.5\pm0.9\mathrm{b}$   | $76.8\pm4.4$ a           |
| Kaila's degree of humification<br>C/N ratio | $19.6\pm1.0~\mathrm{a}$  | $31.7\pm1.7~\mathrm{b}$  | $35.9\pm2.0\mathrm{b}$   | $30.2\pm3.3$ b           |
|   | $19.3\pm0.8~\mathrm{c}$  | $14.8\pm0.2~\mathrm{ab}$ | $16.0\pm0.4~\mathrm{b}$  | $13.5\pm0.2$ a           |
| T-N (%)                                     | $1.84\pm0.07~\mathrm{a}$ | $2.15\pm0.20~\mathrm{a}$ | $2.39\pm0.17~\mathrm{a}$ | $1.69\pm0.45$ a          |
| T-C (%)                                     | $35.5\pm2.5$ b           | $31.5\pm2.5~\mathrm{ab}$ | $38.1\pm2.8~\mathrm{b}$  | $23.0\pm 6.6~\mathrm{a}$ |
| рН (H <sub>2</sub> O, 1:20)                 | $4.23\pm0.05~\mathrm{a}$ | $4.34\pm0.03~\mathrm{a}$ | $4.21\pm0.05~\mathrm{a}$ | $4.36\pm0.07~\mathrm{a}$ |
| Groundwater DOC (mg $L^{-1}$ )              | $19.9\pm3.5~\mathrm{a}$  | $32.0\pm5.8~\mathrm{a}$  | $31.6\pm4.4~\mathrm{a}$  | $30.6\pm0.54~\mathrm{a}$ |

Numbers represent the average  $\pm$  standard error. Numbers within a line followed by different letters differ significantly among the sites. (*p* < 0.05, Tukey-Kramer test).

The averaged water table depth was positively and significantly correlated with  $P_G$ ,  $R_{\text{TOT}}$  and N<sub>2</sub>O, and negatively correlated with NEE and CH<sub>4</sub> (Table S3). Annual NEE in the *Sasa* sites (short- and tall-*Sasa*) showed a significant negative correlation (R = -0.743, p < 0.01) with *Sasa* height (Figure 4), indicating that net CO<sub>2</sub> uptake increased as *Sasa* grew. The annual CH<sub>4</sub> emission including all vegetation was significantly negatively correlated with groundwater DOC (R = -0.618, p < 0.01). The annual N<sub>2</sub>O emission was significantly negatively correlated with the moisture content of the surface peat (R = -0.608, p < 0.01).



**Figure 4.** Relationships between environmental factors and annual GHG budgets. \*\* indicates significant at p < 0.01.

#### 3.5. Estimated Distributions of Vegetation and Environmental Factors Using Satellite Imagery

The water table depth of the *Sasa* and *Ilex* communities tended to be lower than that of the *Sphagnum-Moliniopsis* community in the measurements at the grid points on the southern half of the wetland (Table S4). The *Sasa* height and moisture content of surface peat were significantly correlated with water table depth (R = 0.552, p < 0.01 and R = -0.754, p < 0.01, respectively) (Figure 5 and Table S5). There was a positive, but not significant, correlation between groundwater DOC and water table depth (R = 0.231, p = 0.08).



**Figure 5.** Relationships between averaged water table depth and *Sasa* height, ground water DOC or moisture content of surface peat at grid points. \*\* indicates significant at p < 0.01.

The satellite band values at the grid points and flux measurement plots for each vegetation community are shown in Table S6. The band values (1–4) of the *Sasa* community tended to be higher than those of the other communities. Discriminant analysis using the vegetation communities at the study site (*Sphagnum-Moliniopsis, Moliniopsis-Gale, Sasa, Sasa-Gale, Ilex*) as the objective variable and IKONOS bands 1, 2, 3, 4, NDVI and RVI as explanatory variables showed that the discriminant contributors were bands 1, 2, and 4 (Table S7). Accuracy rate of vegetation classification by discriminant analysis was lowest in the *Sasa-Gale* community (66.7%), but was 100% in the *Sphagnum-Moliniopsis* and *Moliniopsis-Gale* communities. Overall, a 93.6% of accuracy rate was obtained. Figure 6 shows the distribution of vegetation in the entire wetland estimated by the discriminant analysis.



**Figure 6.** Spatial distribution of vegetation communities in the Bibai Wetland estimated using a satellite image.

Multiple regression analysis was conducted by vegetation site using *Sasa* height, water table depth, moisture content of surface peat and groundwater DOC as objective variables and IKONOS band 1, 2, 3, 4, NDVI and RVI as explanatory variables and significant regression equations were established for each (Table S8). For *Sasa* height, all data were used for the analysis. For other environmental factors, 80% of all data were used to create regression equations, and the remaining 20% of data were used to verify the accuracy of the estimates

(see below). Since multiple regressions could not be conducted for the *llex* site due to the small number of data, a single regression was conducted and those with high correlation coefficients were selected. Based on the above regression equation, Figure 7 shows the distributions of *Sasa* height in the *Sasa* sites and environmental factors in the entire wetland estimated from the satellite image bands.





In order to verify the estimation accuracy of the satellite band, the vegetation at 26 sites was surveyed separately from the grid points. Although the accuracy rate for the *Sphagnum-Moliniopsis* community was low, the accuracy rate for the other communities was high, and the overall accuracy rate was 76.9% (Table S9). Bubier et al. (2005) [21] and Heikkinen et al. (2004) [20] reported a vegetation classification accuracy of 80% and 84%, respectively, which are comparable to the values obtained in this study. Environmental factors were relatively well estimated by satellite bands, but the estimated water table depth and groundwater DOC in the *Sasa* site had a narrower range than the measured values (Figure S5).

# 3.6. Estimation of GHG Budget from the Entire Wetland

The area of each vegetation site estimated using satellite bands was 3.86 ha for the *Sphagnum*, 0.122 ha for the short-*Sasa* (height < 50 cm), 17.3 ha for the tall-*Sasa* (50 cm < height

< 150 cm), and 0.210 ha for the *llex*. The net GHG budget for the entire wetland (21.5 ha) was calculated using the GHG budgets for each vegetation site (Table 1), the regression equation between GHG budgets and environmental factors (Figure 5), and the distribution of vegetation and environmental factors estimated using the satellite bands (Figures 6 and 7). The regression equations of *Sasa* height-NEE (for *Sasa* sites), groundwater DOC-CH<sub>4</sub>, and the moisture content of surface peat -N<sub>2</sub>O were used to estimate the respective GHG budget. The NEE of the *Sphagnum* and *llex* sites were calculated by multiplying the annual NEE of each site by the area.

The NEE of CO<sub>2</sub> for the entire wetland was estimated to be  $-42.6 \text{ Mg C y}^{-1}$ , CH<sub>4</sub> to be 0.929 Mg C y<sup>-1</sup>, and N<sub>2</sub>O to be 1.72 kg N y<sup>-1</sup> (Table 3). The net GHG budget of the entire wetland was  $-113 \text{ Mg CO}_2$ -eq y<sup>-1</sup>, and it served as a net GHG sink. The contribution of CO<sub>2</sub> uptake by the tall-*Sasa* site to the total GHG uptake of the wetland was 71% in absolute value, accounting for the majority of the total.

Table 3. GHG budget from the Bibai Wetland estimated by spatial distributions of environmental factors.

| Site   | Sphagnum | Short-Sasa | Tall-Sasa | Ilex    | Entire Wetland |
|--|----------|------------|-----------|---------|----------------|
| Area (ha)  | 3.86     | 0.122      | 17.3      | 0.21    | 21.5           |
| $\frac{1}{\text{CO}_2 (\text{Mg C y}^{-1})}$                 | -1.92    | 0.0561     | -38.7     | -2.07   | -42.6          |
| $CH_4 (Mg C y^{-1})$   | 0.167    | 0.00150    | 0.756     | 0.00432 | 0.929          |
| $N_2O (kg N y^{-1})$   | 0.486    | 0.0141     | 1.11      | 0.103   | 1.72           |
| $\overline{\text{CO}_2 (\text{Mg CO}_2 - \text{eq y}^{-1})}$ | -7.04    | 0.206      | -142      | -7.61   | -156           |
| $CH_4$ (Mg $CO_2$ -eq $y^{-1}$ )                             | 7.58     | 0.0680     | 34.3      | 0.196   | 42.1           |
| $N_2O$ (Mg CO <sub>2</sub> -eq y <sup>-1</sup> )             | 0.227    | 0.00659    | 0.522     | 0.0481  | 0.804          |
| Net GHG $(Mg CO_2$ -eq y <sup>-1</sup> )                     | 0.76     | 0.280      | -107      | -7.36   | -113           |

# 4. Discussion

#### 4.1. Comparison with Previous GHG Flux Measurements

The net ecosystem exchange of CO<sub>2</sub> in soil-plant ecosystems under natural vegetation has been reported to be -154 to -18.9 g C m<sup>-2</sup> y<sup>-1</sup> [37] and -105 to -53.0 g C m<sup>-2</sup> y<sup>-1</sup> [38] (i.e., uptake) in wetlands in western Finland. Heikkinen et al. (2002) [7] reported that NEE varied from -43 (uptake, intermediate fen) to 3 g C m<sup>-2</sup> y<sup>-1</sup> (emission, dry hummock) in the Russian tundra depending on the vegetation and water regime at the site. In the present study, the NEE in the *Sphagnum* site ( $-49.7 \pm 40.2$  g C m<sup>-2</sup> y<sup>-1</sup>) was similar to those reported values, and the NEE in the tall-*Sasa* and *Ilex* sites ( $-240 \pm 80$  and  $-990 \pm 91$  g C m<sup>-2</sup> y<sup>-1</sup>, respectively) were lower (i.e., higher CO<sub>2</sub> uptake) than those reported values.

The NEE of CO<sub>2</sub> over the growing season in forest ecosystems has been reported to be about  $-350 \text{ g C m}^{-2}$  in a Canadian poplar forest [39] and  $-122 \text{ g C m}^{-2}$  in a Finnish birch forest (Leaf area index: LAI = 2.5) [40]. The annual value of NEE was reported to be  $-525 \text{ g C m}^{-2} \text{ y}^{-1}$  for a deciduous mixed forest (LAI = 4.9) in Tennessee, USA [41]. The NEE value of tall-*Sasa* site (LAI = 2.6) in this study was comparable to these reported values.

CH<sub>4</sub> emissions have been reported ranging from 0.1 to 24.7 g C m<sup>-2</sup> y<sup>-1</sup> [37] and 13.1 to 36.0 g C m<sup>-2</sup> y<sup>-1</sup> [38] in wetlands of western Finland, and 2.0 to 16.0 g C m<sup>-2</sup> y<sup>-1</sup> in the Russian tundra [7]. The CH<sub>4</sub> emission of  $11.2 \pm 1.9$  g C m<sup>-2</sup> y<sup>-1</sup> from the *Sphagnum* site in this study was comparable to these reported values.

Martikainen et al. (1993) [17] reported that N<sub>2</sub>O emissions were <4 mg N m<sup>-2</sup> y<sup>-1</sup> from natural wetlands and <4–143 mg N m<sup>-2</sup> y<sup>-1</sup> from drained wetlands in Finland. The N<sub>2</sub>O emission of  $5.05 \pm 4.02$  mg N m<sup>-2</sup> y<sup>-1</sup> for the *Sphagnum* site in this study was comparable to that reported for the natural wetlands. Even the highest N<sub>2</sub>O emission in this study, in the *llex* site (47.2 ± 9.5 mg N m<sup>-2</sup> y<sup>-1</sup>), was lower than the emission from the drained wetland reported previously.

#### 4.2. Spatial Variation of GHG Budgets

Differences in cumulative NEE between sites have been reported to be due to groundwater level, differences in vegetation, and plant biomass [7,9]. The cumulative NEE in this study also showed differences due to vegetation (Table 1). The invasion of shrubby *llex* into the original *Sphagnum* community in our study area increased CO<sub>2</sub> uptake. The NEE in the *Sasa* site was significantly negatively correlated with *Sasa* height (Figure 4), suggesting that the differences in NEE among the plots in the *Sasa* site were due to differences in plant biomass. Increasing *Sasa* biomass increases both the respiratory emission of CO<sub>2</sub> and photosynthetic uptake of CO<sub>2</sub>, but the effect of increasing photosynthesis was greater than that of ecosystem respiration, which is thought to have increased negative NEE (i.e., CO<sub>2</sub> uptake).

The emission pathway of CH<sub>4</sub> from wetland to the atmosphere consists of diffusion of dissolved CH<sub>4</sub> in groundwater along the concentration gradient, transport via aeration tissue (aerenchyma) of aquatic vascular plants, and ascent of CH<sub>4</sub>-containing air bubbles accumulated in peat (i.e., ebullition) [42]. Diffusion may be the dominant pathway for CH<sub>4</sub> emission from peatlands dominated by *Sphagnum* [43,44]. While it has been reported that most of the CH<sub>4</sub> transported by diffusion is oxidized by CH<sub>4</sub> oxidizing bacteria in the unflooded layer of the peat profile [44,45]. Vascular plants, such as sedges, transport CH<sub>4</sub> in peat to the atmosphere through their aerenchyma without undergoing CH<sub>4</sub> oxidation in the aerobic layer, resulting in increased CH<sub>4</sub> fluxes [10,46–50]. Factors that have been reported to control the spatial variation of CH<sub>4</sub> emission from wetlands include groundwater level [12,13], plant biomass [14], and differences in temperature and topography [15].

In this study, the annual CH<sub>4</sub> emission showed a significant negative correlation with water table depth and a significant positive correlation with soil temperature (Table S3). The lowering of the water table depth, which was prominent in the tall-*Sasa* and *Ilex* sites, could cause the aerobic peat layer to thicken. As a result, CH<sub>4</sub> emission was considered to be low due to the lower CH<sub>4</sub> production and enhanced CH<sub>4</sub> oxidation. The high CH<sub>4</sub> emission in the *Sphagnum* site (Table 2), where the water table depth is slightly higher than in the short-*Sasa* site, suggests that the contribution of sedge-mediated CH<sub>4</sub> emission was significant. Possible reasons for decrease in CH<sub>4</sub> emission associated with *Sasa* invasion include reduced gas exchange at the peat surface [32] and the decrease in surface temperature due to ground cover by *Sasa* (Figure 3 and Figure S2) and following decrease in CH<sub>4</sub> production activity.

Although peatlands are considered to emit less N2O in their natural state (i.e., wetland), increased N<sub>2</sub>O emission due to drainage or lowering of the water table caused by climate change has been pointed out [5,17,18]. In this study, the annual N<sub>2</sub>O emission was significantly positively correlated with the water table depth (Table S3), and N<sub>2</sub>O emission was slightly higher in the *llex* site where the water table depth was lower than in the *Sphagnum* site (Table 1). Maljanen et al. (2012) [51] reported that the  $N_2O$  emission from boreal drained peatlands was greater when the C/N ratio of the surface peat was less than 20. They also reported that low soil pH, high nitrate availability and water table depth and addition of mineral soil were also associated with high  $N_2O$  emissions. In this study site, the C/N ratio of the peat at depths of 40 to 150 cm was high (>50). In addition, the peat deeper than 40 cm was almost saturated with groundwater throughout the year (Figure 3), suggesting that N<sub>2</sub>O production in this zone was very limited. In contrast, the C/N ratio of the peat near the surface was lower than 20 (13.5–19.3 for 0–10 cm, Table 2), and the oxygen supply could be sufficient due to long duration without being saturated with groundwater. Therefore, the  $N_2O$  production potential in the surface layer is considered to be high. The C/N ratio of the surface peat in the *llex* site with high  $N_2O$  emission was the lowest among the sites (Table 2). The low T-C content, i.e., low organic matter content in the *llex* site indicates that the peat decomposition is more advanced than in the other sites. In the *llex* site, the surface peat dried out, and the supply of oxygen could accelerate the mineralization of nitrogen and following nitrification, resulting in the emission of  $N_2O$ .

The annual N<sub>2</sub>O emission was also related to  $R_{\text{TOT}}$ ,  $P_{\text{G}}$  and NEE (Table S3). This means that there was a positive correlation between plant biomass (mainly *Sasa*) and N<sub>2</sub>O emission. It has been reported that the rate of decomposition of organic matter and GHG release in peat soils is limited not only by the availability of oxygen, but also by the availability of mineral nutrients (especially N and P) for microbial growth [52,53]. In this study, the lowering of the water table depth could accelerate the decomposition of peat and the mineralization and release of nutrients that had been stored in the organic matter pool [54,55], which could increase plant biomass and increase substrate and microbial activity followed by increasing N<sub>2</sub>O emission.

The study site is characterized by the presence of volcanic tephra mixed with surface peat and high mineral content (Figure 2 and Table 2). It has been suggested that the addition of mineral soil to drained peatland enhances  $N_2O$  emission [51]. In this study, no significant  $N_2O$  emission was observed except for the *llex* site. However, in the future, when the peat is further dried at other sites and the environment becomes more favorable for  $N_2O$  production and emission, the mineral mixed with the peat may promote  $N_2O$  emission.

# 4.3. Sasa Invasion into the Sphagnum-Dominated Wetland

The vegetation in the studied wetland was determined by the water table depth, which was maintained at a high level in the Sphagnum community and lowered in the Sasa and *llex* communities (Figure 3 and Table S4). Sasa height was also correlated with water table depth (Table S4). In the studied field, these environmental changes are thought to have resulted in increased CO<sub>2</sub> uptake due to vegetation invasion and increased plant biomass, as well as changes in surface gas exchange such as decreased CH<sub>4</sub> emission and increased  $N_2O$  emission. Fujimoto et al. (2006) [56] reported that the evapotranspiration rate in the Sphagnum-dominated community was higher than that in the Sasa-dominated community, and that 80-100% of rainfall was consumed by evapotranspiration in the Sphagnum-dominated community and 70–80% of rainfall in the Sasa-dominated community. In the Sarobetsu Mire in northern Hokkaido, where the invasion of Sasa into the Sphagnum vegetation is expanding similarly to the present study site, it has been reported that hydrological conditions such as distance from natural ditches and groundwater flow influenced by drainage and inflow conditions have a significant effect on the expansion of Sasa distribution [26,28]. In addition to the above, considering the fact that the averaged water table depth is lower near the open ditches (Figure 7), the difference in water table depth for each vegetation in the study area is considered to be strongly influenced by the open ditches.

Several studies have shown that climate, hydrology, and nutrient status collectively control the broad distribution of vegetation in northern peatlands (e.g., [57–59]). Nordbakken (1996a, b) [60,61] investigated fine scale variation in vegetation species cover in relation to groundwater level in peatlands in Norway. While many of these studies have estimated species cover, recent studies on carbon and  $CH_4$  exchange and nutrient cycling in peatlands require quantification of plant biomass, such as photosynthetic organs (e.g., [62]). Bubier et al. (2006) [63] investigated the relationship between species and environmental factors in order to improve carbon modeling studies, and reported that groundwater level was significantly positively correlated with leaf biomass and total biomass, soil environment, and GHG fluxes is common, as found in this study, then estimating broad-scale fluxes from satellite-based estimates of vegetation distribution and biomass may be an effective method in peatland ecosystems that are sensitive to environmental changes.

#### 4.4. The Past, Present, and Future of the Bibai Wetland

As a result of the invasion of *Sasa* and *Ilex* into the original *Sphagnum*-diminated vegetation in the Bibai Wetland, the uptake of  $CO_2$  increased, the emission of  $CH_4$  decreased, and the emission of N<sub>2</sub>O slightly increased in the *Ilex* site (Table 1). Net GHG budget changed from emission in the *Sphagnum* site to uptake in the tall-*Sasa* and *Ilex* 

sites. Minkkinen et al. (2002) [64] predicted that draining and reforesting peatlands in Finland would increase  $CO_2$  emission from the soil but greatly increase carbon stocks in tree biomass, reduce  $CH_4$  emission and increase  $N_2O$  emission to a lesser extent, resulting in reduced net GHG emission. The changes in the GHG budget with vegetation change in the wetland shown in this study are consistent with this report.

However, it has also been reported that net ecosystem production (NEP) decreases in older forests in the boreal and temperate zones [65]. Therefore, there is a possibility that the current high CO<sub>2</sub> uptake in the tall-*Sasa* and *Ilex* sites will decrease in the future. In the present Bibai Wetland, CO<sub>2</sub> uptake has increased by 5 and 20 times, respectively, due to the invasion of *Sasa* and *Ilex* into the original *Sphagnum*-dominated community (Table 1), but at the same time progressing peat decomposition due to the lowering of the water table depth is also presented (Table 2 and Table S4). Furthermore, the NEE in the short-*Sasa* site was  $124 \pm 43$  g C m<sup>-2</sup> y<sup>-1</sup>, suggesting net CO<sub>2</sub> emission. Therefore, it is expected that carbon emission from the peat was dominant in the process of invasion and establishment of short-*Sasa* into the original *Sphagnum*-diminated vegetation, leading to the present tall-*Sasa*.

Before 1960s, most of the wetland had been occupied by *Sphagnum*-dominated vegetation [29]. The carbon accumulation rate of the entire wetland (21.5 ha) at the time estimated by current carbon exchange rate (CO<sub>2</sub> uptake by NEE-CH<sub>4</sub> emission) in the *Sphagnum* site was 8.26 Mg C y<sup>-1</sup>. In contrast, the current carbon accumulation rate of the entire wetland was 41.7 Mg C y<sup>-1</sup> (Table 3), which was about five times higher than the estimated rate for *Shsagnum*-dominated wetland due to the invasion of *Sasa* and *Ilex*, which increased carbon fixation. However, in this study, we did not separate peat decomposition (microbial respiration) from plant respiration, nor did we measure the supply of plant matter to the peat as litter. Therefore, the amount of peat decomposition due to the invasion of *Sasa*, and the contribution of carbon fixed by plants to new peat formation is not clear. A further understanding of the carbon cycle between the atmosphere, plants, and peat is needed.

#### 5. Conclusions

The net GHG budget of the entire wetland where dwarf bamboo (*Sasa*) has invaded the original *Sphagnum*-dominated vegetation was estimated by combining the measurement of GHG fluxes by vegetation and the estimation of the distribution of environmental factors using satellite imagery. The net GHG budget for the entire wetland was estimated to be  $-113 \text{ Mg CO}_2$ -eq y<sup>-1</sup>, acting as a net source of GHG. The CO<sub>2</sub> uptake by the tall-*Sasa* accounted for 71% of the total, indicating the importance of the accuracy enhancement on estimation for biomass and CO<sub>2</sub> balance of *Sasa*. Consequently, drawdown of water table followed by invasion of *Sasa* and *Ilex* into *Sphagnum*-dominated wetland increased carbon accumulation to the wetland ecosystem and changed it from a source to a sink for GHG at present.

The site studied here is an example that lowering of water table of soils with high organic matter content will not always lead to carbon loss from the ecosystem because the  $CO_2$  uptake by developing vegetation can more than compensate the possible C loss from the soil.

**Supplementary Materials:** The following are available online at https://www.mdpi.com/article/ 10.3390/atmos12040448/s1, Figure S1: Vegetation of the study field (Bibai Wetland), Table S1: Correlation coefficients between GHG fluxes and environmental factors; Figure S2: Seasonal changes in air temperature, precipitation and snow depth (a: line, black and grey bars, respectively), soil temperature at 3cm depth (b), water table depth in a *Sphagnum* plot (c) and PAR (photosynthetically active radiation) (d), Table S2: Parameters for estimating total ecosystem respiration ( $R_{TOT}$ ) and gross photosynthesis ( $P_G$ ); Figure S3: Relationships between soil temperature at 3cm depth and total ecosystem respiration at each measurement plot, Table S3: Correlation coefficients between annual GHG budgets and environmental factors; Figure S4: Relationships between photosynthetically active radiation (PAR) and gross photosynthesis / monthly air temperature at each measurement plot, Table S4: Water table depth, physico-chemical properties of surface peat layer (0–10 cm) and ground water DOC (dissolved organic carbon) at grid points; Figure S5: Relationships between measured values of environmental factors and their estimated values using satellite bands, Table S5: Correlation coefficients among environmental factors at grid points; Table S6: Satellite image band values for each vegetation community; Table S7: Accuracy rate of vegetation classification by discriminant analysis; Table S8: Coefficients of multiple regression analysis of environmental factors using satellite image bands; Table S9: Verification of vegetation classification and *Sasa* height estimation using satellite bands.

**Author Contributions:** A.K., F.T., O.N. and R.H. conceived and designed the experiments; A.K., F.T. and O.N. performed the field measurements; A.K. analyzed the data; M.T. contributed analysis of satellite imagery; A.K. and F.T. wrote the paper; R.H. gave many constructive comments on this manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Acknowledgments: The authors would like to thank the staff members of the Hokkaido Agricultural Research Center, National Agriculture and Food Research Organization and the members of the Laboratory of Soil Science, Faculty of Agriculture, Hokkaido University for their support with the measurement and management of the study field.

Conflicts of Interest: The authors declare no conflict of interest.

#### References

- 1. Gorham, E. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecol. Appl.* **1991**, *1*, 182–195. [CrossRef] [PubMed]
- 2. Turnen, J.; Pitkanen, A.; Tahvanainen, T.; Tolonen, K. Carbon accumulation in West Siberian mires, Russia. *Glob. Biogeochem. Cycles* **2001**, *15*, 285–296.
- 3. Clymo, R.S. The limits of peat bog growth. Philos. Trans. R. Soc. Lond. B 1984, 303, 605–654.
- 4. Intergovernmental Panel on Climate Change (IPCC). The physical science basis: Anthropogenic and natural radiative forcing. In *Climate Change 2013*; Myhre, G., Shindell, D., Eds.; Cambridge University Press: Cambridge, UK, 2013.
- 5. Kasimir-Klemedtsson, A.; Klemedtsson, L.; Berglund, K.; Martikainen, P.; Silvola, J.; Oenema, O. Greenhouse gas emissions from farmed organic soils: A review. *Soil Use Manag.* **1997**, *13*, 245–250. [CrossRef]
- 6. Schimel, D.; House, J.I.; Hibbard, K.A.; Bousquet, P.; Ciais, P.; Peylin, P.; Braswell, B.H.; Apps, M.J.; Baker, D.; Bondeau, A. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* **2001**, *414*, 169–172. [CrossRef]
- 7. Heikkinen, J.E.P.; Elsakov, V.; Martikainen, P.J. Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in NE Europe, Russia. *Glob. Biogeochem. Cycles* **2002**, *16*, 1115. [CrossRef]
- 8. Bubier, J.L.; Bhatia, G.; Moore, T.R.; Roulet, N.T.; Lafleur, P.M. Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems* **2003**, *6*, 353–367.
- 9. Bubier, J.L.; Frolking, S.; Crill, P.M.; Linder, E. Net ecosystem productivity and its uncertainty in a diverse boreal peatland. *J. Geophys. Res.* **1999**, *104*, 27683–27692. [CrossRef]
- Christensen, T.R.; Joabsson, A.; Ström, L.; Panikov, N.; Mastepanov, M.; Öquest, M.; Svensson, B.H.; Nykänen, H.; Martikainen, P.J.; Oskarsson, H. Factors controlling large-scale variations in methane emissions from wetlands. *Geophys. Res. Lett.* 2003, 30, 1414. [CrossRef]
- 11. Shurpali, N.J.; Verma, S.B.; Clement, R.J.; Billesbach, D.P. Seasonal distribution of methane flux in a Minnesota peatland measured by eddy correlation. *J. Geophys. Res.* **1993**, *98*, 20649–20655. [CrossRef]
- 12. Shurpali, N.J.; Verma, S.B. Micrometeorological measurements of methane flux in a Minnesota peatland during two growing seasons. *Biogeochemistry* **1998**, *40*, 1–15. [CrossRef]
- 13. Liblik, L.K.; Moore, T.R. Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, Northwest Territories, Canada. *Glob. Biogeochem. Cycles* **1997**, *11*, 485–494. [CrossRef]
- 14. Bellisario, L.M.; Bubier, J.L.; Moore, T.R.; Chanton, J.P. Controls on CH<sub>4</sub> emissions from a northern peatland. *Glob. Biogeochem. Cycles* **1999**, *13*, 81–91. [CrossRef]
- 15. Macdonald, J.A.; Fowler, D.; Hargreaves, K.J.; Skiba, U.; Leithe, I.D.; Murray, M.B. Methane emission rates from a northern wetland; response to temperature, water table and transport. *Atmos. Environ.* **1998**, *32*, 3219–3227. [CrossRef]
- 16. Regina, K.; Silvola, J.; Martikainen, P.J. Short-term effects of changing water table on N<sub>2</sub>O fluxes from peat monoliths from natural and drained boreal peatlands. *Glob. Chang. Biol.* **1999**, *5*, 183–189. [CrossRef]
- 17. Martikainen, P.J.; Nykänen, H.; Crill, P.; Silvola, J. Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. *Nature* **1993**, *366*, 51–53. [CrossRef]
- Martikainen, P.J.; Nykiinen, H.; Alm, J.; Silvola, J. Changes in fluxes on carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophy. *Plant Soil* 1995, 168–169, 571–577. [CrossRef]
- 19. Nykänen, H.; Alm, J.; Lang, K.; Silvola, J.; Martikainen, P.J. Emissions of CH<sub>4</sub>, N<sub>2</sub>O and CO<sub>2</sub> from a virgin fen and a fen drained for grassland in Finland. *J. Biogeogr.* **1995**, *22*, 351–357. [CrossRef]

- 20. Heikkinen, J.E.P.; Virtanen, T.; Huttunen, J.T.; Elsakov, V.; Martikainen, P.J. Carbon balance in East European tundra. *Glob. Biogeochem. Cycles* **2004**, *18*, GB1023. [CrossRef]
- 21. Bubier, J.; Moore, T.; Savage, T.; Crill, T. A comparison of methane flux in a boreal landscape between a dry and a wet year. *Glob. Biogeochem. Cycles* **2005**, *19*, GB1023. [CrossRef]
- 22. Armentano, T.V.; Menges, E.S. Patterns of change in the carbon balance of organic soil-wetlands of the temperate zone. *J. Ecol.* **1986**, *74*, 755–774. [CrossRef]
- 23. Fujita, H.; Igarashi, Y.; Hotes, S.; Takada, M.; Inoue, T.; Kaneko, M. An inventory of the mires of Hokkaido, Japan—Their development, classification, decline, and conservation. *Plant Ecol.* **2009**, *200*, 9–36. [CrossRef]
- 24. Fujimura, Y.; Fujita, H.; Kato, K.; Yanagiya, S. Vegetation dynamics related to sediment accumulation in Kushiro Mire, northeastern Japan. *Plant Ecol.* **2008**, *199*, 115–124. [CrossRef]
- Oki, K.; Awadu, T.; Oguma, H.; Omasa, K. Spatial assessment of the alder tree in Kushiro mire, Japan using remotely sensed imagery—effects of the surrounding land use on Kushiro mire. *Environ. Monit. Assess.* 2005, 109, 243–253. [CrossRef]
- 26. Fujimura, Y.; Fujita, H.; Takada, M.; Inoue, T. Relationship between hydrology and vegetation change from *Sphagnum* lawns to vascular plant *Sasa* communities. *Landsc. Ecol. Eng.* **2012**, *8*, 215–221. [CrossRef]
- Takada, M.; Mishima, Y.; Natsume, S. Estimation of surface soil properties in peatland using ALOS/PALSAR. *Landsc. Ecol. Eng.* 2009, 5, 45–58. [CrossRef]
- Takada, M.; Inoue, T.; Mishima, Y.; Fujita, H.; Hirano, T.; Fujimura, Y. Geographical assessment of factors for *Sasa* expansion in the Sarobetsu Mire, Japan. *J. Landsc. Ecol.* 2012, *5*, 58–71. [CrossRef]
- 29. Kasubuchi, T.; Miyaji, N.; Kohyama, K.; Yanagiya, S. The water conditions of the Bibai wetland and the investigation of its conservation method. *Jpn. J. Soil Sci. Plant Nutr.* **1994**, *65*, 326–333, (In Japanese with English Summary).
- 30. Miyaji, N.; Ooi, N.; Noshiro, S.; Fujine, H.; Kohyama, K.; Kasubuchi, T.; Yanagiya, S. Formation process and vegetation history of the Bibai Peatland, central Hokkaido, Japan, during the Holocene. *Jpn. J. Hist. Bot.* **2000**, *8*, 15–31, (In Japanese with English Summary).
- Nagata, O.; Takakai, F.; Hatano, R. Effect of Sasa invasion on global warming potential in Sphagnum dominated poor fen in Bibai, Japan. Phyton 2005, 45, 299–307.
- 32. Takakai, F.; Nagata, O.; Hatano, R. Effect of *Sasa* invasion on CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O fluxes in Sphagnum dominated poor fen in Bibai, Hokkaido, Japan. *Phyton* **2005**, *45*, 319–326.
- 33. Tokida, T.; Miyazaki, T.; Mizoguchi, M.; Nagata, O.; Takakai, F.; Kagemoto, A.; Hatano, R. Falling atmospheric pressure as a trigger for methane ebullition from peatland. *Glob. Biogeochem. Cycles* **2007**, *21*, GB2003. [CrossRef]
- 34. Tokida, T.; Mizoguchi, M.; Miyazaki, T.; Kagemoto, A.; Nagata, O.; Hatano, R. Episodic release of methane bubbles from peatland during spring thaw. *Chemosphere* **2007**, *70*, 165–171. [CrossRef] [PubMed]
- Kondo, R.; Endo, K. Various indices for determining the degree of decomposition and some physico-chemical properties of peat soils. *Pedologist* 1993, 37, 41–56, (In Japanese with English Summary).
- 36. Kaila, A. Determination of the degree of humification in peat samples. Agric. Food Sci. 1956, 28, 18–35. [CrossRef]
- Nykänen, H.; Heikkinen, J.E.P.; Pirinen, L.; Tiilikainen, K.; Martikainen, P.J. Annual CO<sub>2</sub> exchange and CH<sub>4</sub> fluxes on a subarctic palsa mire during climatically different years. *Glob. Biogeochem. Cycles* 2003, 17, 1018. [CrossRef]
- 38. Alm, J.; Talanov, A.V.; Saarnio, S.; Silvola, J.; Ikkonen, E.; Aaltonen, H.; Nykänen, H.; Martikainen, P.J. Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia* **1997**, *110*, 423–431. [CrossRef]
- Black, T.A.; den Hartog, G.; Neumann, H.H.; Blanken, P.D.; Yang, P.C.; Russel, C.; Nesic, Z.; Lee, X.; Chen, S.G.; Staebler, R.; et al. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Glob. Chang. Biol.* 1996, 2, 219–229. [CrossRef]
- 40. Aurela, M.; Tuovinen, J.P.; Laurila, T. Net CO<sub>2</sub> exchange of a subarctic mountain birch ecosystem. *Theor. Appl. Climatol.* **2001**, *70*, 135–148. [CrossRef]
- 41. Greco, S.; Baldocchi, D. Seasonal variations of CO<sub>2</sub> and water vapour exchange rates over a temperate deciduous forest. *Glob. Chang. Biol.* **1996**, *2*, 183–197. [CrossRef]
- 42. Whiting, G.J.; Chanton, J.P.; Bartlett, D.S.; Happell, J.D. Relationship between CH<sub>4</sub> emission, biomass, and CO<sub>2</sub> exchange in a subtropical grassland. *J. Geophys. Res.* **1991**, *96*, 13067–13071. [CrossRef]
- Chasar, L.S.; Chanton, J.P.; Glaser, P.H.; Siegel, D.I. Methane concentration and stable isotope distribution as evidence of rhizosphereic processes: Comparison of a fen and bog in the Glacial Lake Agassiz Peatland complex. *Ann. Bot.* 2000, *86*, 655–663. [CrossRef]
- 44. Frenzel, P.; Karofeld, E. CH4 emission from a hollow-ridge complex in a raised bog: The role of CH4 production and oxidation. *Biogeochemistry* **2000**, *51*, 91–112. [CrossRef]
- Raghoebarsing, A.A.; Smolders, A.J.P.; Schmid, M.C.; Rijpstra, W.I.C.; Wolters-Arts, M.; Derksen, J.; Jetten, M.S.; Schouten, S.; Damsté, J.S.S.; Lamers, L.P.; et al. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. *Nature* 2005, 436, 1153–1156. [CrossRef]
- 46. Whiting, G.J.; Chanton, J.P. Plant-dependent CH<sub>4</sub> emission in subarctic Canadian fen. *Glob. Biogeochem. Cycles* **1992**, *6*, 225–231. [CrossRef]
- 47. Waddington, J.M.; Roulet, N.T.; Swanson, R.V. Water table control of CH<sub>4</sub> emission enhancement by vascular plants in boreal peatlands. *J. Geophys. Res.* **1996**, *101*, 22775–22785. [CrossRef]

- 48. King, J.Y.; Reeburgh, W.S.; Regli, S.R. Methane emission and transport by arctic sedge in Alaska: Results of a vegetation removal experiment. *J. Geophys. Res.* **1998**, *103*, 29083–29092. [CrossRef]
- 49. Joabsson, A.; Christensen, T.R.; Wallen, B. Vascular plant controls on methane emission from northern peatforming wetlands. *Trends Ecol. Evol.* **1999**, *14*, 385–388. [CrossRef]
- 50. Christensen, T.; Panikov, N.; Mastepanov, M.; Joabsson, A.; Stewart, A.; Oquist, M.; Sommerkorn, M.; Reynaud, S.; Svensson, B. Biotic controls on CO<sub>2</sub> and CH<sub>4</sub> exchange in wetlands—A closed environment study. *Biogeochemistry* **2003**, *64*, 337–354. [CrossRef]
- 51. Johnson, L.C.; Damman, A.W.H. Decay and its regulation in *Sphagnum* peatlands. *Adv. Bryol.* **1993**, *5*, 249–296.
- 52. Maljanen, M.; Shurpali, N.; Hytönen, J.; Mäkiranta, P.; Aro, L.; Potila, H.; Laine, J.; Li, C.; Martikainen, P.J. Afforestation does not necessarily reduce nitrous oxide emissions from managed boreal peat soils. *Biogeochemistry* **2012**, *108*, 199–218. [CrossRef]
- 53. Aerts, R.; van Logtestijn, R.; van Staalduinen, M.; Toet, S. Nitrogen supply effects on productivity and potential leaf litter decay of Carex species from peatlands differing in nutrient limitation. *Oecologia* **1995**, *104*, 447–453. [CrossRef] [PubMed]
- 54. Nadelhoffer, K.J.; Gibhn, A.E.; Shaver, G.R.; Laundre, J.A. Effects of temperature and substrate quality on element mineralization in six Arctic soils. *Ecology* **1991**, 72, 242–253. [CrossRef]
- 55. Freeman, C.; Lock, M.A.; Reynolds, B. Impacts of climatic change on peatland hydrochemistry: A laboratory-based experiment. *Chem. Ecol.* **1993**, *8*, 49–59. [CrossRef]
- 56. Fujimoto, T.; Iiyama, I.; Sakai, M.; Nagata, O.; Hasegawa, S. Comparison of evapotranspiration between indigenous vegetation and invading vegetation in a bog. *Jpn. Soc. Soil Phys.* **2006**, *103*, 39–47, (In Japanese with English Summary).
- 57. Vitt, D.H.; Chee, W.L. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetation* **1990**, *89*, 87–106. [CrossRef]
- 58. Glaser, P.H. Raised bogs in eastern North America—Regional controls for species richness and floristic assemblages. *J. Ecol.* **1992**, *80*, 535–554. [CrossRef]
- 59. Gignac, L.D.; Gauthier, R.; Rochefort, L.; Bubier, J. Distribution and habitat niches of 37 peatland Cyperaceae species across a broad geographic range in Canada. *Can. J. Bot.* **2004**, *82*, 1292–1313. [CrossRef]
- 60. Nordbakken, J.F. Fine-scale patterns of vegetation and environmental factors on an ombrotrophic mire expanse: A numerical approach. *Nord. J. Bot.* **1996**, *16*, 197–209. [CrossRef]
- 61. Nordbakken, J.F. Plant niches along the water-table gradient on an ombrotrophic mire expanse. *Ecography* **1996**, *19*, 114–121. [CrossRef]
- 62. Frolking, S.; Roulet, N.T.; Moore, T.R.; Lafleur, P.M.; Bubier, J.L.; Crill, P.M. Modeling the seasonal to annual carbon balance of Mer Bleue bog, Ontario, Canada. *Glob. Biogeochem. Cycles* **2002**, *16*, 1030. [CrossRef]
- 63. Bubier, J.; Moore, T.R.; Crosby, G. Fine-scale vegetation distribution in a cool temperate peatland. *Can. J. Bot.* **2006**, *84*, 910–924. [CrossRef]
- 64. Minkkinen, K.; Korhonen, R.; Savolainen, I.; Laine, J. Carbon balance and radiative forcing of Finnish peatlands 1900–2100-the impact of forestry drainage. *Glob. Chang. Biol.* **2002**, *8*, 785–799. [CrossRef]
- 65. Pregitzer, K.S.; Euskirchen, E.S. Carbon cycling and storage in world forests: Biome patterns related to forest age. *Glob. Chang. Biol.* **2004**, *10*, 2052–2077. [CrossRef]