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Primary vegetation recovery following fifteen years of alien plant control on the subtropical oceanic island of Anijima, Ogasawara

Running head: Alien Plant Control and Vegetation Recovery

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ABSTRACT

Evaluation is essential in alien plant control projects aimed at restoring native vegetation. However, restoration targets often encompass a constellation of diverse ecosystems due to environmental variability, and identifying the most appropriate reference ecosystem for each site remains a challenge. Comprehensive evaluations that address this complexity are rare. In this study, we developed a novel analytical approach to assess vegetation recovery in detail and applied globally recognized restoration attributes to evaluate a long-term control project in Anijima Island in the subtropical oceanic Ogasawara Islands. The project aimed to restore primary dry scrub forests, grasslands, and bare lands, by removing alien plants. We used original vegetation survey data and time-series data collected throughout the project. Two reference ecosystem settings were applied: one assessed native cover recovery and alien cover reduction, without considering canopy structure or species composition, suitable for early-stage evaluation; the other assessed the complete recovery of primary vegetation, based on species abundance and vertical stratification, suitable for later-stage evaluation. Although the project significantly reduced total alien plant cover, a notable re-increase of alien plant species was also observed. Some native species showed recovery in herb and shrub layers. However, full ecosystem recovery was not detected within the 15-year monitoring period, suggesting that longer-term project may be required to capture the full trajectory of restoration.

Key Words: bare rock and grassland landscape, ecosystem constellation, forest landscape, oceanic islands, restore forest ecosystems, reference ecosystem

Introduction

Evaluation is a crucial component of restoration projects and has therefore been the subject of active discussion (SER 2004; Ruiz-Jaen 2005; Wortley et al. 2013; Hallet et al. 2019; Mazón et al. 2019; Prach et al. 2019). The reference ecosystem targeted by restoration is typically not a single specific ecosystem, but rather a constellation of ecosystems with varying species composition and spatial structure that reflect environmental heterogeneity (SER 2004). Similarly, the ecosystem under restoration is also a constellation of diverse ecosystems, shaped by different initial states at the start of the project, varying patterns of species immigration during the restoration process, diverse restoration practices and stages, and heterogeneous environmental conditions (Brudvig et al. 2019). Although there have been conceptual discussions, few studies have explicitly addressed how to identify the corresponding reference ecosystem among multiple native ecosystems for a given restoration site.

Anijima, the largest uninhabited subtropical oceanic island in the World Natural Heritage of Ogasawara Islands in the Northwest Pacific Ocean, has various environments such as dry scrub forest, bare ground, grassland, and areas with varying levels of alien plant invasions forming a constellation of ecosystems. In this study, we evaluated an alien plant control project in Anijima aimed at restoring native ecosystems. To support practical restoration efforts, we conducted a comprehensive evaluation by developing a novel analytical approach for assessing detailed vegetation recovery and introducing internationally recognized restoration attributes.

Numerous endemic species have established unique ecosystems on oceanic islands like Anijima, which have never been connected to a continent (Emerson 2002; Caujapé-Castells et al. 2010). These ecosystems are particularly vulnerable to invasive alien species due to their isolation and the sensitivity of their biota (Paulay 1994). Alien plant invasions often lead to rapid biodiversity loss on islands, occurring at rates that exceed those on the mainland (Whittaker & Fernandez-Palacios 2007). Consequently, the restoration of native ecosystems on oceanic islands is urgent, and alien plant control is actively pursued in several locations (Cuevas and Zalba 2010; Gardener et al. 2010; Tanaka et al. 2010; Meyer et al. 2019). For our evaluation, we used both original vegetation survey data and time-series vegetation data obtained the project.

Clearly defining a reference ecosystem is essential for evaluating restoration project (Prach et al. 2019). Some previous studies do not explicitly define reference ecosystems, though their evaluation procedures imply certain standards. One group assumed that higher species diversity and vegetation cover indicated better restoration, without considering species composition (Loh and Daehler 2008; Jäger and Kowarik 2010). A second group compared canopy structure to that of well-developed stands as the reference (Harada and Yagasaki 2019). A third group used indicator species to assess closeness to reference ecosystems (Jírová et al. 2012). A fourth group defined constellation of many reference ecosystems in ordination space and compared the position of the constellation of many recovering ecosystems accordingly (Brudvig et al. 2019) but does not consider recovery at the level of individual plots.

The objective of this project was to restore primary ecosystems at each individual recovering site. Given the diversity of environments on the island—from bare land to dry shrubland and forest—the dissimilarity between reference ecosystems and each restoration site must be explicitly evaluated. We employed two reference ecosystem settings: one to assess native cover recovery and alien cover reduction without considering canopy structure or species composition (suitable for early-stage evaluation), and another to assess full recovery of primary vegetation with comparable species abundance and vertical stratification (appropriate for later-stage evaluation). To evaluate complete recovery of primary vegetation, we used ordination based on species cover in each vertical stratum (canopy, shrub, etc.) and added an axis representing total vegetation cover. The first two axes were used to minimize noise from higher dimensions. In alien plant control, saplings may reach 100% cover at the forest floor, which must be distinguished from full canopy cover, thus requiring stratified analysis. Our reference ecosystems also include primary bare land. In the ordination procedures, the bare land plots are placed at the coordinate origin, where many average communities cluster. The additional axis representing standardized total cover helps distinguish such plots.

In addition to detailed evaluation of vegetation recovery, we conducted a comprehensive assessment based on nine commonly used restoration attributes worldwide (SER 2004; Ruiz-Jaen and Aide 2005; Mazón et al. 2019): (1) species assemblages, (2) indigenous species, (3) functional groups, (4) physical conditions, (5) ecological functions, (6) landscape interactions and integrity, (7) external threats, (8) ecosystem resilience, and (9) self-sustainability. Socioeconomic attributes (Hallet et al. 2019) were not considered in this study because Anijima Island is part of the World Natural Heritage Site, where restoration of primary vegetation is essential for maintaining its socioeconomic and conservation value.

This study presents the first comprehensive evaluation of native ecosystem restoration following severe alien plant invasion on a subtropical oceanic island in the North Pacific. Our objectives were to evaluate native ecosystem recovery using original and project monitoring vegetation data, propose a detailed vegetation evaluation approach suitable for ecosystem constellations, and incorporate internationally recognized restoration attributes for comprehensive project assessment.

Materials and methods

Research sites

The Ogasawara Islands, located in the Pacific Ocean approximately 1,000 km from the Japanese mainland, are home to a diverse array of endemic species (Japanese Government, 2010). Human settlement on the Ogasawara Islands began in the early 19th century, initially serving as a port of call for Western whalers. After the islands were declared Japanese territory in 1876, the government promoted settlement and cultivation by introducing various alien plant species (Tanimoto et al. 1995; Nobushima 2010; Toyoda 2014). Anijima, the largest uninhabited island in the Ogasawara Archipelago, spans approximately 7.87 km². It remains a largely pristine natural area, with dry scrub forests that have never been permanently settled by humans (Shimizu et al. 1991; Shinozawa et al. 1993). The entire island has been designated as a World Natural Heritage Site (Fig. 1). Dominant native species in the dry scrub forests of Anijima include *Planchonella obovata* (R.Br.) Pierre, *Schima wallichii* (DC.) Korth. subsp. *mertensiana* (Siebold et Zucc.) Bloemb., and the endemic *Distylium lepidotum* Nakai. Endemic and endangered species also present include *Psychotria homalosperma* A.Gray, *Planchonella boninensis* (Nakai) Masam. et Yanagihara, and *Calanthe hattorii* Schltr. (Miyawaki 1989; Shimizu 2008; Ogasawara Islands Branch Office 2013). In bare rock and grassland areas, dominant species vary widely across sites and include *Osteomeles schwerinae* C.K.Schneid., the endemic *Syzygium cleyerifolium* (Yatabe) Makino, and other endemic species such as *Fimbristylis longispica* var. *boninensis* (Hayata) Ohwi. These areas also harbor endangered species, such as *Callicarpa parvifolia* Hook. et Arn., *Crepidiastrum grandicollum* (Koidz.) Nakai, and *Sedum boninense* Yamam. ex Tuyama (Miyawaki 1989; Shimizu 2008; Ogasawara Islands Branch Office 2013). Non-forested areas, such as bare rock and grasslands, represent some of the original landscapes of Anijima (Tokyo Forestry Bureau 1939). However, the primary vegetation in these areas is being altered by the spread of alien trees such as *Casuarina equisetifolia* L. and *Pinus luchuensis* Mayr, which are transforming dry, non-forested areas into forests (Tanimoto et al. 1995; Tomiyama 1998;

Fujinuma et al. 2008). Additionally, alien shrub species such as *Lantana camara* subsp. *aculeata* and various herbaceous species, including Poaceae grasses, have become established in bare rock and grassland habitats.

Control project for alien plants

Anijima has a high conservation priority due to its extensive native vegetation. Alien plant control has been implemented across a wide area since 2009 and is ongoing as of 2024. Efforts have focused primarily on the plateau in the central region of the island, where many rare plant and animal species occur. The main targets for control were tall alien tree species such as *C. equisetifolia* and *P. luchuensis*, which rapidly expand within and around dry shrublands and bare land, transforming these areas into tall forests. All individuals found were treated. Shrub species, including *L. camara* subsp. *aculeata* and similar taxa, were also targeted when found in areas undergoing alien tree removal. Workers conducted ground surveys on foot, recorded the coordinates of target alien plants using GPS devices, and applied the following removal methods (Table 1): Herbicide (Roundup Maxload; Nissan Chemical Corporation, Tokyo, Japan) was injected into the stems of large alien trees. For narrower stems, herbicide was applied to the cut surfaces after the main stem was felled. Small alien plants, including tree seedlings and herbaceous species, were removed manually (Fig. S1). Following the initial control efforts, repeated treatments were conducted in areas where alien plants reestablished. The map of the project area is presented in Seto et al. (2025, preprint). The dominance of controlled alien plant species in each plot is shown in Supplementary Tables S3 and S4.

Vegetation survey data

At several control sites, vegetation surveys were conducted to obtain relevé data (vegetation survey records) before the removal of alien plants, and these surveys were repeated periodically to monitor the recovery of primary vegetation following alien plant control. Post-control vegetation surveys were carried out every few years, with regrowth of target alien plants removed immediately after each monitoring survey. Time-series vegetation survey data were obtained from control project reports prepared by contractors commissioned by the government (Ogasawara Islands Branch Office 2014, 2015, 2016; Kanto Regional Forest Office 2021a, 2022, 2023, 2024; Japan Forest Technology Association 2022, 2023) (Fig. 2). Because the control project lacked sufficient long-term monitoring, non-time-series data were supplemented by the author through additional surveys of previously controlled sites where vegetation surveys had not originally been conducted. Surveys were also carried out in non-control sites with heavy alien invasion (defined as native species cover <70% of total cover) to serve as "before control" data. These included a variety of environments such as forests, bare rock, and grasslands areas. The "immediately after initial control" condition was estimated by removing target alien species from the "before control" data, reflecting the fact that workers eliminated all individuals of the targeted alien species during initial control. Non-control sites with minimal alien invasion (defined as native species cover ≥70% and alien species cover <10% in all layers) were surveyed to provide baseline data on primary vegetation, designated as “reference native vegetation.” Additional vegetation surveys were conducted between 2011 and 2023. In all vegetation surveys, quadrats of 2–10 m^2 were established, depending on vegetation height. The cover of each species was recorded based on the Braun-Blanquet approach (Braun-Blanquet 1964) for each vertical layer (I: canopy, II: sub-canopy, III: shrub, and IV: herb) and using six foliage cover classes (+: <1%, 1: 1–10%, 2: 10–25%, 3: 25–50%, 4: 50–75%, and 5: 75–100%). For analysis, we focused on sites where control primarily targeted the two alien trees, *C. equisetifolia* and *P. luchuensis*, as there were too few sites originally aimed at controlling other dwarf alien species such as *L. camara* subsp. *aculeata*, but such species were removed if found within the alien tree control plots.

Landscape division based on historical maps

Primary landscapes currently dominated by alien plants were classified based on historical vegetation maps from the Tokyo Forestry Bureau (1939) (Fig. 1, Table S1). At that time, no vegetation category was dominated by alien plants, indicating little to no alien plant invasion. Due to the low spatial resolution of these historical maps, a single vegetation category often encompassed multiple vegetation types. The historical “vegetation map” represented the dominant vegetation type in each landscape, rather than fine-scale vegetation details. Importantly, the historical map was not used as a restoration target but instead served to define broader landscape categories. Each category was thus treated as a *landscape type*, encompassing a range of vegetation types. For the purposes of analysis, we focused on two primary landscape types: the “Forested landscape” and the “Bare rock and grassland landscape” (non-forested landscape). Coastal forests and other areas with limited spatial extent were excluded due to the insufficient number of vegetation survey sites.

Plant community ordination

Due to the wide range of vegetation types on the island, performing a single, unified analysis of species composition and dominance across all habitats was difficult, as few species were common across different landscapes. Therefore, vegetation analyses were conducted separately within each landscape category—specifically the Forested landscape and the Bare rock and grassland landscape.

Principal component analysis (PCA) was performed using all relevé (vegetation survey data) available within each landscape type, including: reference native vegetation (restoration target), vegetation before control, vegetation immediately after initial control (with alien plants removed), and vegetation several years after control. PCA was based on plant species cover data using the six Braun-Blanquet cover classes (+, 1, 2, 3, 4, and 5), with "+" replaced by a value of 0.5. Each species in each vertical stratum (I: canopy, II: sub-canopy, III: shrub, IV: herb) was treated as a separate variable, allowing for the differentiation between high cover in the canopy versus on the forest floor (e.g., seedlings). The PCA was conducted using the prcomp function in R Ver. 4.2.3 (R Core Team), and vegetation at each study site was plotted in a two-dimensional principal component space defined by the first two axes (PC1 and PC2).

Evaluating recovery

Two approaches were used to evaluate the recovery of native vegetation. The first focused on assessing increases in native species cover alongside reductions in alien species cover. The second was a composite evaluation that combined total vegetation cover with the two-dimensional vegetation-PCA. Dissimilarity between each managed plot and its corresponding reference native vegetation was evaluated within a three-dimensional composite space, with two-dimensional vegetation-PCA and one-dimensional total vegetation cover. Additionally, a simplified evaluation was performed by excluding the total vegetation cover axis from the second one, considering only the two-dimensional vegetation-PCA space.

Recovery assessed by native and alien species covers using qualitative regression

We summed the coverage of all canopy strata for each species in each relevé. The dataset consisted of both time-series and non-time-series data, with effects distinguished by plot and treatment in the following qualitative regression analysis.

$$Cover_{kj} = cover\_plot\_effect_{km} + cover\_treatment\_effect_{kn} + cover\_intercept_{k} \quad (1)$$

Here, $Cover_{kj}$ is the vegetation cover of relevé j, with k representing native or alien species. The $cover\_plot\_effect_{km}$ is the effect of plot m, and the stochastic distribution among plots was assumed to be a normal distribution with a zero mean value and standard deviation. The $cover\_treatment\_effect_{kn}$ is the effect of treatment type n (reference native vegetation, before control, immediately after initial control, after initial control <5 years, and ≥5 years), and stochastic distribution of $cover\_treatment\_effect_{kn}$ among treatments was also assumed as normal distribution with zero mean value and a standard deviation. The $cover\_intercept_{k}$ is the regression intercept, assumed to be normally distributed with a mean and standard deviation. A large $cover\_treatment\_effect_{kn}$ for native species and a small $cover\_treatment\_effect_{kn}$ for alien species represented good vegetation. Covers of native and alien species in forests and bare rock and grassland landscapes were analyzed. The stochastic modeling system RStan (https://mc-stan.org/users/interfaces/rstan) was used for all qualitative regressions.

Recovery of species composition and relative dominance using qualitative regression

To evaluate restoration quality in terms of vegetation structure (species composition and dominance), we used PCA based on vegetation data. By restricting the analysis to the first two PCA axes, we reduced noise from higher-dimensional variation. Anijima features a diverse range of environments, from forests with deep soil to bare rock, grasslands, and shrublands. Restoration goals (i.e., primary vegetation, including primary bare land) vary by site. However, in some areas, native ecosystems have been supplanted by alien forests, rendering the restoration goals unclear. Complex environments, including variations in local soil depth due to rocks, hinder statistical niche modeling based on digital elevation models and current geological maps. In this study, we considered the smallest dissimilarity between the focal restoration relevé and various relevés of the reference native vegetation within each landscape as the indicator of restoration quality. Smaller dissimilarity values indicated greater proximity to the restoration goal. The dissimilarity between the focal relevé j and the nearest relevé of the reference native vegetation within the landscape, $PCAdissimilarity_{j}$, was determined using the two-dimensional vegetation-PCA space as the Euclidean distance. Qualitative regression analysis was performed using RStan software.

$$\mathit{PCAdissimilarity}_j = \mathit{PCAdissimilarity\_plot\_effect}_m + \mathit{PCAdissimilarity\_treatment\_effect}_n + \mathit{PCAdissimilarity\_intercept} \tag{2}$$

Here, $\mathit{PCAdissimilarity\_plot\_effect}_m$ is the effect of plot *m*. The stochastic distribution was assumed to be a normal distribution with zero mean value and standard deviation. The $\mathit{PCAdissimilarity\_treatment\_effect}_n$ is the effect of treatment type *n* (before control, immediately after initial control, after initial control <5 years, and ≥5 years), and stochastic distribution was also assumed as normal distribution with zero mean value and a standard deviation. The *PCAdissimilarity_intercept* is the regression intercept, assumed to be normally distributed with a mean and standard deviation. A Small $\mathit{PCAdissimilarity\_treatment\_effect}_n$ represents good vegetation.

Recovery of species composition, relative dominance, and the total cover by qualitative regression

Primary bare land is a critical habitat for the endangered endemic tiger beetle *Cicindela bonina* (Nakane et Kurosawa), making it a key target in restoration. However, bare land is difficult to evaluate using PCA alone, which is based on relative dominance. To better capture its characteristics, we introduced a third axis for total vegetation cover, defined as the sum of cover values across all strata, standardized by the mean and standard deviation across relevés. Each relevé was thus mapped into a three-dimensional composite space (PC1 and PC2 from the vegetation PCA, plus standardized total vegetation cover). The minimum dissimilarity between the focal relevé *j* and the nearest relevé of the reference native vegetation within the landscape, $\mathit{CMPdissimilarity}_j$, was determined using the three-dimensional composite space as the Euclidean distance. Qualitative regression analysis was performed using RStan software.

$$\mathit{CMPdissimilarity}_j = \mathit{CMPdissimilarity\_plot\_effect}_m + \mathit{CMPdissimilarity\_treatment\_effect}_n + \mathit{CMPdissimilarity\_intercept} \tag{3}$$

The $\mathit{CMPdissimilarity\_plot\_effect}_m$ represents the effect of plot *m*. The stochastic distribution was assumed to be a normal distribution with a zero mean value and standard deviation. The $\mathit{CMPdissimilarity\_treatment\_effect}_n$ is the effect of treatment type *n* (before control, immediately after initial control, after initial control <5 years, and ≥5 years), and stochastic distribution was also assumed as normal distribution with zero mean value and standard deviation. The *CMPdissimilarity_intercept* is the regression intercept assumed to be normally distributed with a mean and standard deviation. A small $CMPdissimilarity\_treatment\_effect_n$ represents good vegetation.

Native and alien species recruitment after control using semi-quantitative regression

The recruitment and regrowth of native and alien species were examined in relation to the progression of the control project. To assess recruitment, we focused on species cover in the shrub (III) and herb (IV) layers. To detect trends over the course of the project, we employed a semi-quantitative approach, assigning ordinal values to project stages as follows: 0 = "before control," 1 = "immediately after initial control," 2 = "after initial control <5 years," and 3 = "after initial control ≥5 years". These stages (0–3) represent ordinal variables; however, appropriate statistical methods for trend detection in ordinal data are limited. Therefore, we treated stages as continuous numeric variables and applied generalized linear models (GLMs) using linear regression in R (https://www.r-project.org/). Native and alien species covers were used as dependent variables, with the project stage as the independent variable. A linear term was included to identify directional trends, and a quadratic term was added to detect potential non-linear patterns, such as a rebound in alien species cover during the later stages. A successful restoration trajectory would be reflected by a continuous increase in native species cover and a continuous decrease in alien species cover. Conversely, an unsuccessful trajectory may involve a temporary decline in alien species immediately after control, followed by a rebound, or the absence of significant native species recruitment. Species selected for analysis included representative species of primary native vegetation and dominant invasive alien species across both the forest landscape and the bare rock and grassland landscape (Table S2).

Results

We obtained data from 104 plots (19 monitoring plots) and 165 relevé plots (Tables S3 and S4).

Vegetation ordination

In the forest landscape, the reference native vegetation was characterized by the native tree *Rhaphiolepis indica* (L.) Lindl. var. *umbellata* (Thunb.) H.Ohashi, *D. lepidotum*, and *P.*

obovate (Fig. 3). Degraded forests were generally positioned opposite the reference native vegetation along PC1, with *C. equisetifolia* and *P. luchuensis* as representative species. In the bare rock and grassland landscape, dwarf scrub vegetation, *O. schwerinae*, and the rock-dwelling sedge *F. longispica* var. *boninensis* were observed. Taller vegetation dominated by *D. lepidotum*, *P. obovate*, and *S. cleyerifolium* was distinct from the dwarf scrub. Alien vegetation, including *C. equisetifolia* and the native *Trema orientalis* (L.) Blume, was prominent. Some "before control" plots with high alien species cover exhibited species compositions similar to reference native vegetation, indicating ongoing invasion.

Change in native and alien plant cover during the project

Reference native vegetation exhibited greater native species cover than the control project plots in the forest landscape; however, significant recovery was not detected (Fig. 4). In the bare rock and grassland landscapes, no significant differences in native cover were observed between reference native vegetation and project plots, or among the different project stage. Alien species cover, however, showed significant change. In both landscapes, reference native vegetation had minimal alien cover, whereas "before control" plots had the highest alien cover (Fig. 4). Alien cover decreased to the level of reference vegetation immediately after the initial control but increased significantly in later years. Current alien species cover (≥5 years) was significantly higher than immediately after initial control in both landscapes, suggesting rebound through recruitment.

Recovery of species composition and relative dominance

Dissimilarity from reference native vegetation, in terms of species composition and relative dominance (based on vegetation-PCA), did not show significant recovery in the forest landscape. However, the control project contributed significantly to recovery in the bare rock and grassland landscape (Fig. 5). When total cover was incorporated into the analysis, a rebound effect was observed in the forest landscape. No significant effects were detected in the bare rock and grassland landscapes under this composite metric.

Individual species in the undergrowth

In the forest landscape, native climax-dominant trees and shrubs such as *D. lepidotum* and *S. wallichii* increased over time, whereas the pioneer tree *T. orientalis* declined (Table 2). In the bare rock and grassland landscapes, the native creeping shrub *O. schwerinae* and the endangered sedge *F. longispica* var. *boninensis* increased, but the canopy-dominant *P. obovate* declined. Among alien species, *P. luchuensis* decreased in the forest landscape, but a rebound was observed in *C. equisetifolia* (Table 3). In the bare rock and grassland landscapes, *C. equisetifolia* also declined, whereas alien Poaceae grasses increased.

Discussion

In general, significant effects of alien plant invasion on native vegetation were detected by comparisons between reference and before control vegetations, and before control and immediately after control vegetations. The project significantly reduced the total cover of alien plants; however, a notable re-increase in alien cover after initial control was also observed. Although some native species showed recovery in the herb and shrub layers, significant recovery of the native ecosystem as a whole was not detected in this study—likely because a 15-year monitoring period is too short to capture full ecosystem restoration. Shimizu (2023) demonstrated that the primary shrubland dominant, *D. lepidotum*, on Anijima requires more than 100 years to develop into an upper-layer tree with a 10-cm trunk diameter, suggesting that canopy recovery may take a century or more. Our results suggest that continued alien plant control is essential to suppress reinvasion, and that restoring native ecosystems may require long-term commitment over several decades to centuries.

Vegetation data in Anijima alien plant control project

The 1939 vegetation map is one of the oldest in Japan and represents a significant asset for this project. However, its low spatial resolution created difficulties in defining reference ecosystems at the 10 m plot level. Traditional vegetation surveys were limited to a small number of points that are characteristic of each vegetation type, and thus insufficient to reconstruct the full distribution of native ecosystems across the island. Within the alien plant control project, time-series data were collected from 19 plots to assess recovery of natural vegetation. These data are valuable for evaluating vegetation recovery at the plot level, but they are insufficient to assess recovery across the entire project area, particularly for minor vegetation types that could not be analyzed. Project contractors selected time-series plots from among many alien control sites. Typically, contractors have an incentive to report positive recovery outcomes. Therefore, it is recommended that the government assign the control and monitoring tasks (for example, establishment and evaluation of time-series plots) to separate contractors and ensure an adequate budget for monitoring.

Evaluation approach for the constellation of ecosystems

In our rigorous evaluation approach, we defined restoration success as achieving the same species abundance and vertical structure as the reference ecosystem. Minor variability was reduced using the first two major axes in the ordination. Because vegetation characteristics vary by site, a constellation approach, that is, evaluating each plot in relation to the closest matching reference site, is necessary. To our knowledge, this is the first study to define the nearest reference vegetation in ordination space as the target for restoration assessment.

An alternative approach involves building distribution models that predict species abundance at each vertical stratum based on environmental conditions as commonly used species distribution models (Seto et al. 2025, preprint). However, such detailed models have not yet been established (Bonthoux et al. 2013). Both reference and recovering ecosystems should be viewed as constellations. When using average responses in a two-dimensional ordination space, the mean values may be close to the target vegetation, but high site-to-site variability can make this misleading. Techniques such as PERMDISP (Permutational Analysis of Multivariate Dispersion) and PERMANOVA (Permutational Multivariate Analysis of Variance) can assess variance differences between reference and recovering ecosystems in multivariate space (Anderson and Walsh 2013). However, these analyses require that both constellations are derived from the same geographic area; biased sampling in one group renders such comparisons invalid. In our study, the primary reference ecosystem was unclear at several sites; hence, this method was not applied.

We also adopted a simpler method using the total cover of native and alien species. This method detected reinvasion by alien species, whereas the constellation-based method did not, likely because the latter captured shifts involving fast-growing natives like *T. orientalis*, in addition to alien species. The simpler approach may be more suitable in early project stages to detect reductions in alien cover, whereas the constellation method may be better suited for later stages to evaluate convergence toward primary vegetation. Future study should further examine the robustness of the constellation analysis to noise and determine the optimal number of ordination dimensions.

General attributes commonly used for restoration evaluation

We evaluated general attributes of restoration to provide a comprehensive assessment of the project (SER 2004; Ruiz-Jaen and Aide 2005; Mazón et al. 2019).

(1) species assemblages

Our constellation analysis based on PCA incorporated species assemblage information, though it did not distinguish canopy structures separately. The recovering ecosystems have not yet reached the reference communities. Alien species cover decreased during the project but subsequently re-increased.

(2) indigenous species

Some native plant species characteristic of the climax forest on Anijima showed signs of recovery in the herb and shrub layers (Table 2).

(3) functional groups

Although functional group information is potentially embedded in the PCA-based constellation analysis, we did not explicitly analyze it. The project successfully removed alien trees that caused physiognomic shifts on primary bare land. In forest landscapes, *T. orientalis*—a pioneer species—temporarily dominated immediately after control, then gradually declined (Table 2). This pattern is typical after disturbance or during early succession and does not necessarily indicate restoration failure.

(4) physical conditions

We did not explicitly assess physical conditions. However, factors such as forest floor light availability and litter thickness are known to influence species composition and native species establishment in the Ogasawara Islands (Hata et al. 2010; Kanto Regional Forest Office 2024). The observed recovery of native and pioneer species at the forest floor suggests a temporary improvement in light availability due to the project.

(5) ecological functions

Ecological functions were not explicitly evaluated. However, physiognomic shifts caused by alien tree invasion from bare land to forest may have significantly altered ecosystem functions. Since our goal was to restore the primary ecosystem, a decline in forest ecosystem services and an increase in erosion due to the removal of alien trees may be acceptable. Recovery of native and pioneer species at the forest floor suggests a short-term reduction in forest ecosystem services. Notably, control of *C. equisetifolia* has been reported to increase soil moisture (Hata et al. 2016), indicating potential change in ecosystem functions such as water cycling.

(6) landscape interactions and integrity

Although landscape-scale considerations were not explicitly addressed, future evaluations should incorporate them. In the Ogasawara Islands, speciation and genetic differentiation have occurred in genera such as *Pittosporum*, *Symplocos*, *Callicarpa*, and *Elaeocarpus*, driven by diverse microhabitats within the small islands (Sugai et al. 2013). Steep genetic clines are likely maintained by the interaction between gene flow and selective pressures from varied habitats. Maintaining or restoring the original primary ecosystem landscape is essential for in situ conservation of these genetically distinct populations.

(7) external threats

Although restoration aims to establish self-sustaining and resilient ecosystems (Ruiz-Jaen 2005), continuous invasion by alien species remains the most significant external threat. This study detected a post-control rebound in alien species, including expansion of alien Poaceae grasses. These findings emphasize the need for continued monitoring and adaptive management based on surrounding vegetation conditions. A UAV-based study in the Ogasawara Islands (Seto and Koike 2025) also suggested that alien plant invasions are not yet saturated on uninhabited islands, raising concerns about future invasions or new introductions from inhabited areas.

(8) ecosystem resilience

Native forests have demonstrated resistance to some aggressive alien species, such as *L. camara* subsp. *aculeata* (Seto et al. 2025 preprint; Aung and Koike 2015). Early control before alien species significantly modify native forests remains an effective strategy, especially in forest landscapes.

(9) self-sustainability

Post-control vegetation does not yet show sufficient self-sustainability against reinvasion by alien species. Notably, *C. equisetifolia* was observed to regain cover over time after initial removal, indicating the need for ongoing management. Field surveys on cliffs and landslide areas (Seto & Koike 2025) suggested that inaccessible areas not covered by the control project may serve as reservoirs for reinvasion.

Conclusions

Although alien plant invasions significantly affected native vegetation and were reduced by the control project, reinvasion after initial removal was also considerable. Significant recovery of the native ecosystem was not observed, possibly because the 15-year monitoring period was too short to capture full ecosystem restoration. Data remain insufficient, particularly for minor ecosystem types. Based on general restoration attributes widely applied internationally, future project phases should address challenges such as the invasion of new alien species and the presence of inaccessible habitats (e.g., cliffs and landslide areas), which may serve as persistent sources of reinvasion.

Declarations

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Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

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Supporting Information

The following supplementary materials are available in the online version of this article:

Fig. S1: Photographs of control project

Table S1: Vegetation categories from the historical 1939 vegetation map and the landscape categories used in this study.

Table S2: Species analyzed for changes across different stages of the control project.

Table S3: Vegetation survey data collected from forest landscapes.

Table S4: Vegetation survey data collected from bare rock and grassland landscapes.

Table S5: Details of the linear trends in native species across control project stages, analyzed using semi-quantitative linear regression.

Table S6: Details of the linear trends in alien species across control project stages, analyzed using semi-quantitative linear regression.

Table S7: Details of the rebound trends in alien species across control project stages, analyzed using semi-quantitative quadratic regression.

Tables

Table 1: Major alien plant species and control methods on Anijima Island. *Pinus luchuensis* is effectively controlled by felling the main stem; thus, a "Cut" method is used rather than the "Cut and Paint" method.

Alien plants dominant before the initial control	Invaded primary vegetation	Method of control	Repeat intervals for control
Casuarina equisetifolia	Bare rocky ground, Grassland, Dry scrub forest, Along the coast	Tree stem injection with herbicides; Cutting stem and painting herbicides; Pulling sapling out	Every 5–6 years in areas of significant conservation importance where rare species exist
Pinus luchuensis	Bare rocky ground, Grassland, Dry scrub forest	Tree stem injection with herbicides; Cutting stem only due to less sprout; Pulling sapling out	Every 5–6 years in areas of significant conservation importance where rare species exist
Lantana camara subsp. *aculeata*	Bare rocky ground, Grassland, Forest edge, Gaps in dry scrub forests	Large stem injection with herbicides; Cutting stem and painting herbicides; Pulling out; Herbicide spraying	Coincide with tall alien tree control
Alien Poaceae grass	Bare rocky ground, Grassland	No control has been carried out.	No control has been carried out.

Table 2: Semi-quantitative trend regression of native species recovery by project stages and species cover. Details are presented in Table S5. *$p < 0.05$, ** $p < 0.001$

Landscape	Species and stratum	Linear trend
Forest	III *Trema orientalis*	Decrease*
Forest	IV *Planchonella obovata*	Ns
Forest	IV *T. orientalis*	Ns
Forest	IV *Distylium lepidotum*	Increase**
Forest	IV *Rhaphiolepis indica* var. *umbellata*	Ns
Forest	IV *Schima wallichii*	Increase*
Bare rock and grassland	IV *P. obovate*	Decrease*
Bare rock and grassland	IV *T. orientalis*	Ns
Bare rock and grassland	IV *D. lepidotum*	Ns
Bare rock and grassland	IV *Osteomeles schwerinae*	Increase**
Bare rock and grassland	IV *Syzygium cleyerifolium*	Ns
Bare rock and grassland	IV *Fimbristylis longispica* var. *boninensis*	Increase*

Table 3: Semi-quantitative quadratic regression of alien species rebound by project stages and species cover. Details are provided in Tables S6 and S7. * $p < 0.05$, ** $p < 0.001$

Landscape	Species and stratum	Linear effect	Rebound as positive quadratic term
Forest	III *C. equisetifolia*	Ns	Rebound* (lowest between immediate after initial control to <5 years)
Forest	III *P. luchuensis*	Decrease*	Ns
Forest	IV *L. camara* subsp. *aculeata*	Ns	Ns
Forest	IV *C. equisetifolia*	Ns	Rebound* (lowest between immediate after initial control to <5 years)
Forest	IV *P. luchuensis*	Decrease*	Ns
Bare rock and grassland	III *C. equisetifolia*	Decrease**	Ns
Bare rock and grassland	III *P. luchuensis*	Ns	Ns
Bare rock and grassland	IV *C. equisetifolia*	Ns	Ns
Bare rock and grassland	IV *P. luchuensis*	Ns	Ns
Bare rock and grassland	IV Alien Poaceae grass	Increase**	Ns

Figure legends

Figure 1: Location of Anijima in the Northwest Pacific. (a) Location of the Ogasawara Archipelago in the Northwest Pacific Ocean, (b) Location of Chichijima Islands, including Anijima, within the Ogasawara Archipelago, and (c) Original landscape types and current research plots based on the historical 1939 vegetation map. The green area in (b) indicates a World Natural Heritage area.

Figure 2: Categories of vegetation data. The data include "immediately after initial control," derived from the "before control" data.

Figure 3: Principal component analysis (PCA) of relevé from (a) forest landscape (29% contribution) and (b) bare rock and grassland landscape (35% contribution). Arrows in the diagram represent the principal component loadings of speciesthat are significantly correlated with PC1 and PC2, with green indicating native species and red indicating alien species. Labels in the diagram indicate the stratum and species names. AP: Alien Poaceae grass, CE: *Casuarina equisetifolia*, DL: *Distylium lepidotum*, FL: *Fimbristylis longispica* var. *boninensis*, LC: *Lantana camara* subsp. *aculeata*, OS: *Osteomeles schwerinae*, PL: *Pinus luchuensis*, PO: *Planchonella obovate*, RI: *Rhaphiolepis indica* var. *umbellate*, SC: *Syzygium cleyerifolium*, TO: *Trema orientalis*. Arrows for Alien Poaceae grass indicate represent mean principal component loadings of *Bothriochloa bladhii* var. *bladhii*, *Paspalum scrobiculatum* var. *orbiculare,* and *Sporobolus diandrus*.

Figure 4: Effect of control stages on native and alien plant covers. Shown are the $cover\_treatment\_effect_{kn}$ values as defined in equation 1. (a) represents native species in forest landscapes, (b) represents alien species in forest landscapes, (c) represents native species in bare rock and grassland landscapes, and (d) represents alien species in bare rock and grassland landscapes. Different letters in the figure indicate significant differences among groups. Vertical bars represent the standard deviation.

Figure 5: Effect of control stages on vegetation-PCA dissimilarity from reference native vegetation, evaluated using Equation 2 as $PCAdissimilarity\_treatment\_effect_n$, is shown in (a) and (b), representing forest and bare rock and grassland landscapes, respectively. Combined dissimilarity to reference native vegetation, evaluated using Equation 3 as

CMPdissimilarity_treatment_effect$_n$, is shown in (c) and (d), also representing forest and bare rock and grassland landscapes, respectively. Different letters in the figure indicate significant differences among groups. Vertical bars represent the standard deviation.

Figures

Fig. 1

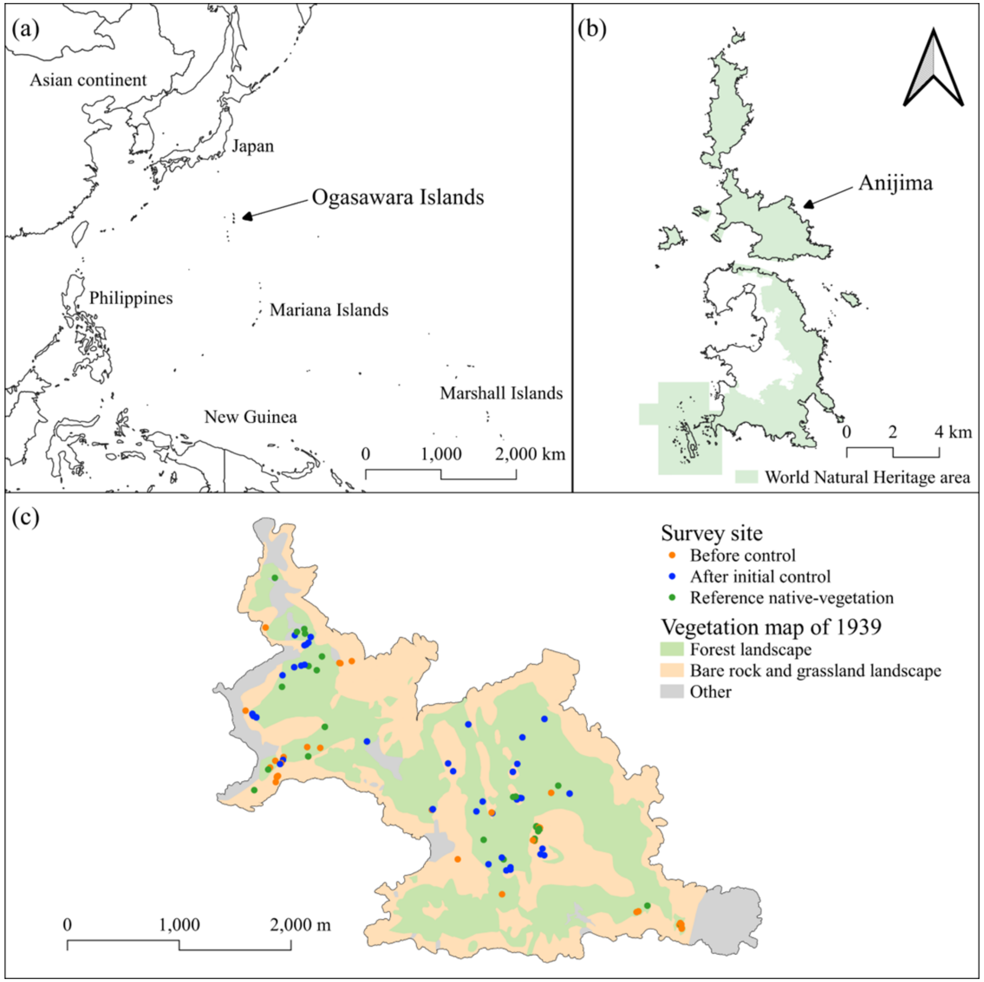


Fig. 2

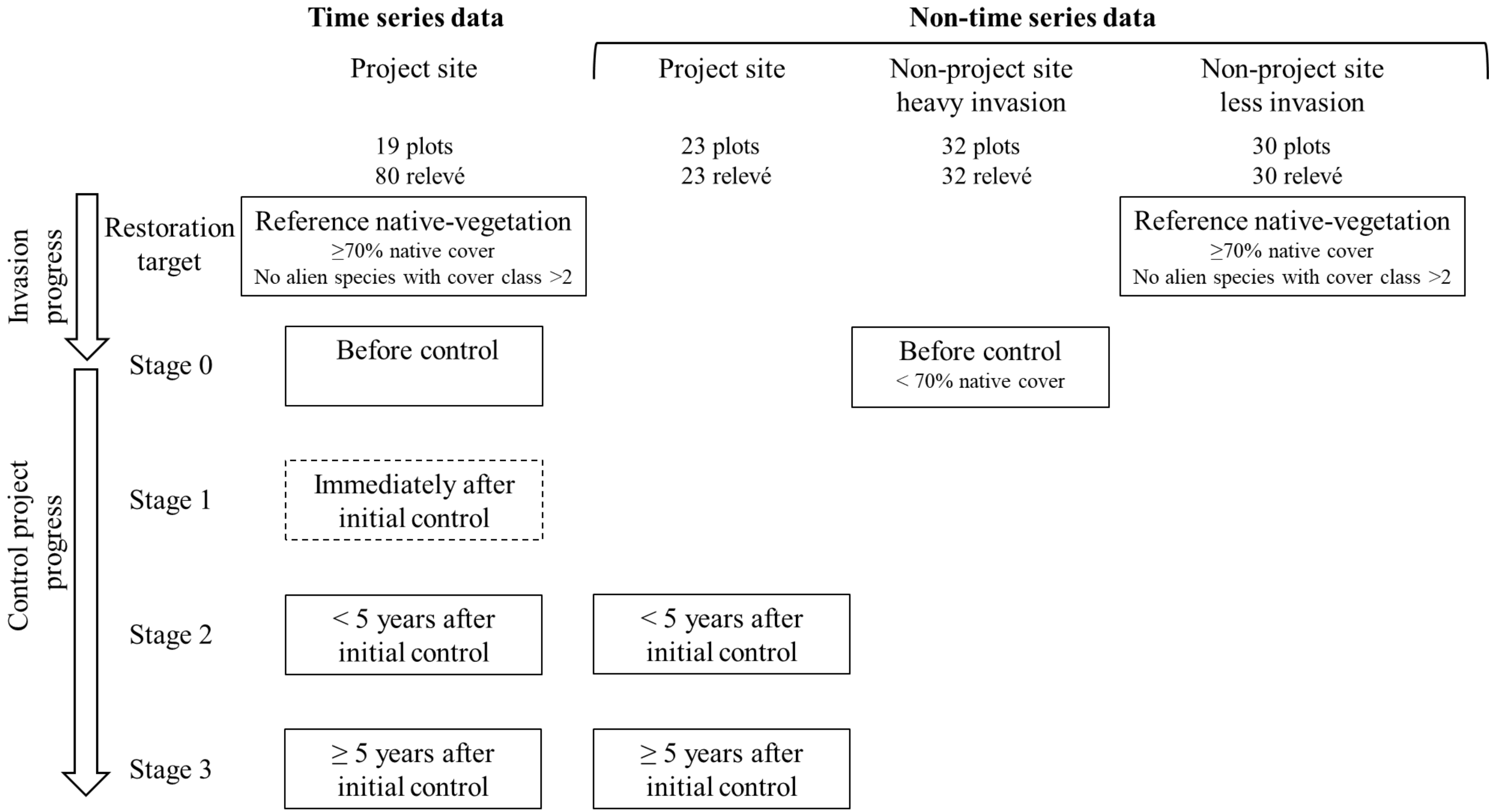

Time series data
Non-time series data
Project site
Project site
Non-project site heavy invasion
Non-project site less invasion
19 plots
80 relevé
23 plots
23 relevé
32 plots
32 relevé
30 plots
30 relevé
Invasion progress
Control project progress
Restoration target
Reference native-vegetation
≥70% native cover
No alien species with cover class >2
Reference native-vegetation
≥70% native cover
No alien species with cover class >2
Stage 0
Before control
Before control
< 70% native cover
Stage 1
Immediately after initial control
Stage 2
< 5 years after initial control
< 5 years after initial control
Stage 3
≥ 5 years after initial control
≥ 5 years after initial control

Fig. 3

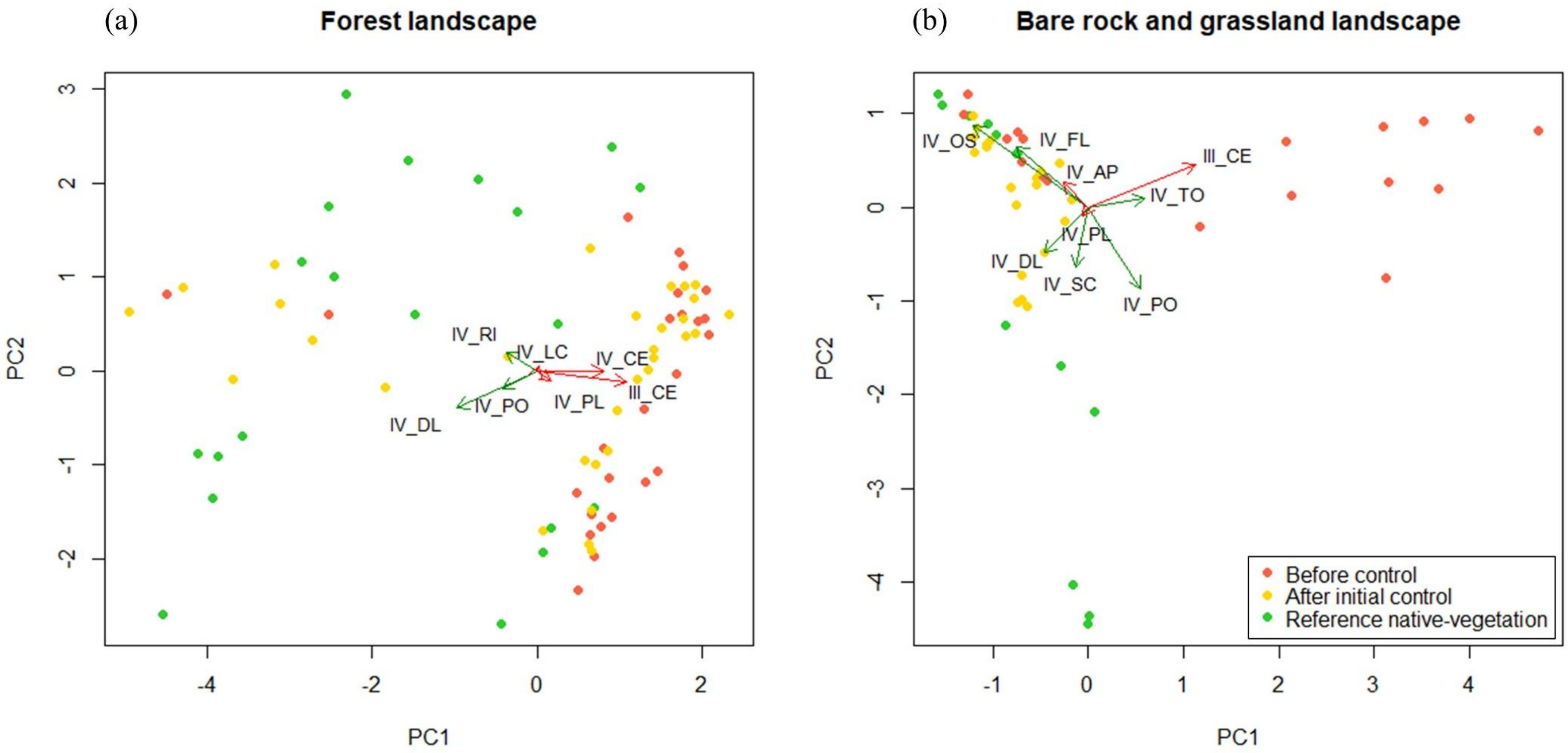

(a)
Forest landscape
PC1
PC2
IV_RI
IV_LC
IV_CE
III_CE
IV_PL
IV_PO
IV_DL
(b)
Bare rock and grassland landscape
PC1
PC2
IV_OS
IV_FL
III_CE
IV_AP
IV_TO
IV_PL
IV_DL
IV_SC
IV_PO
Before control
After initial control
Reference native-vegetation

Fig. 4

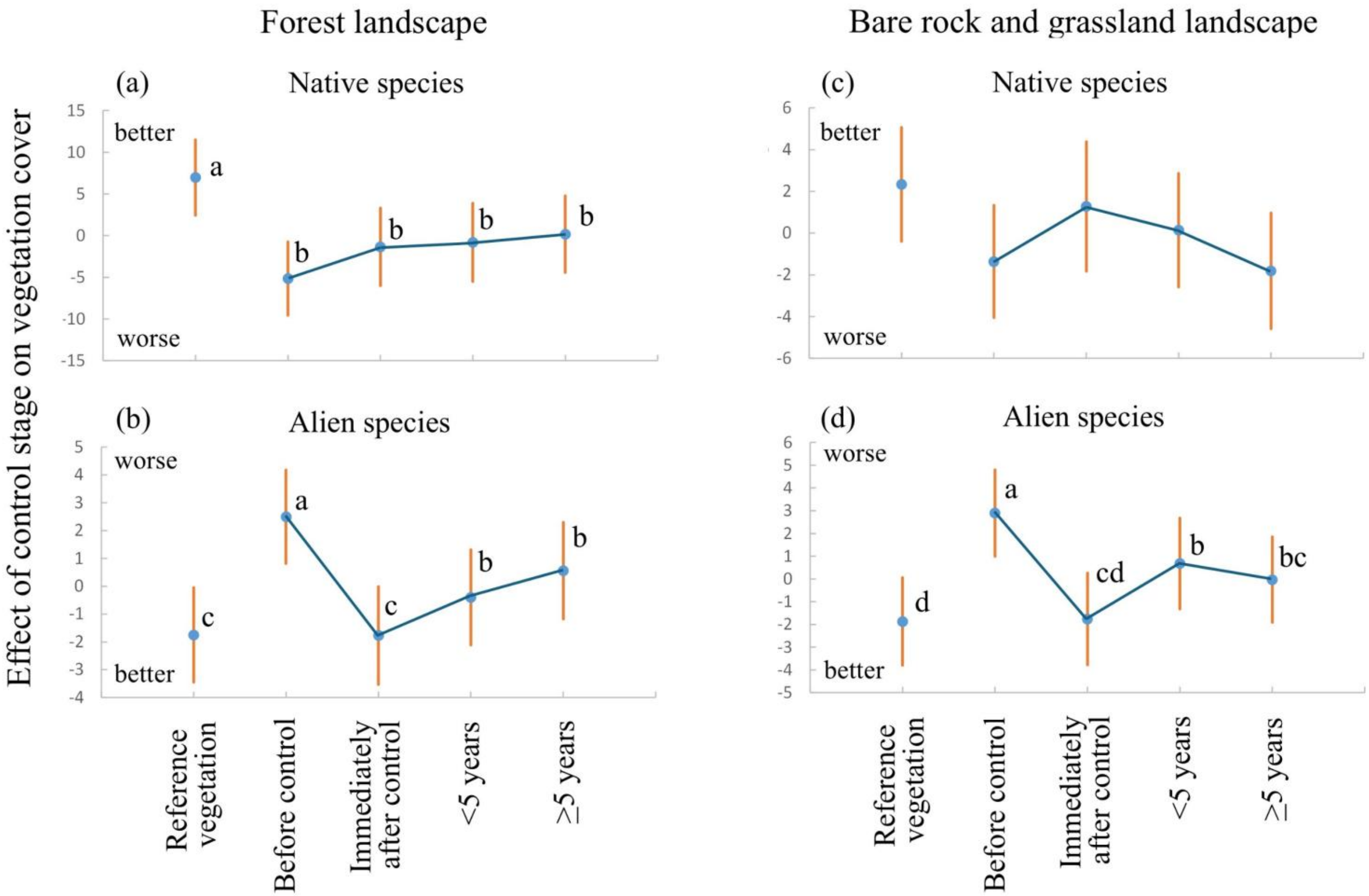
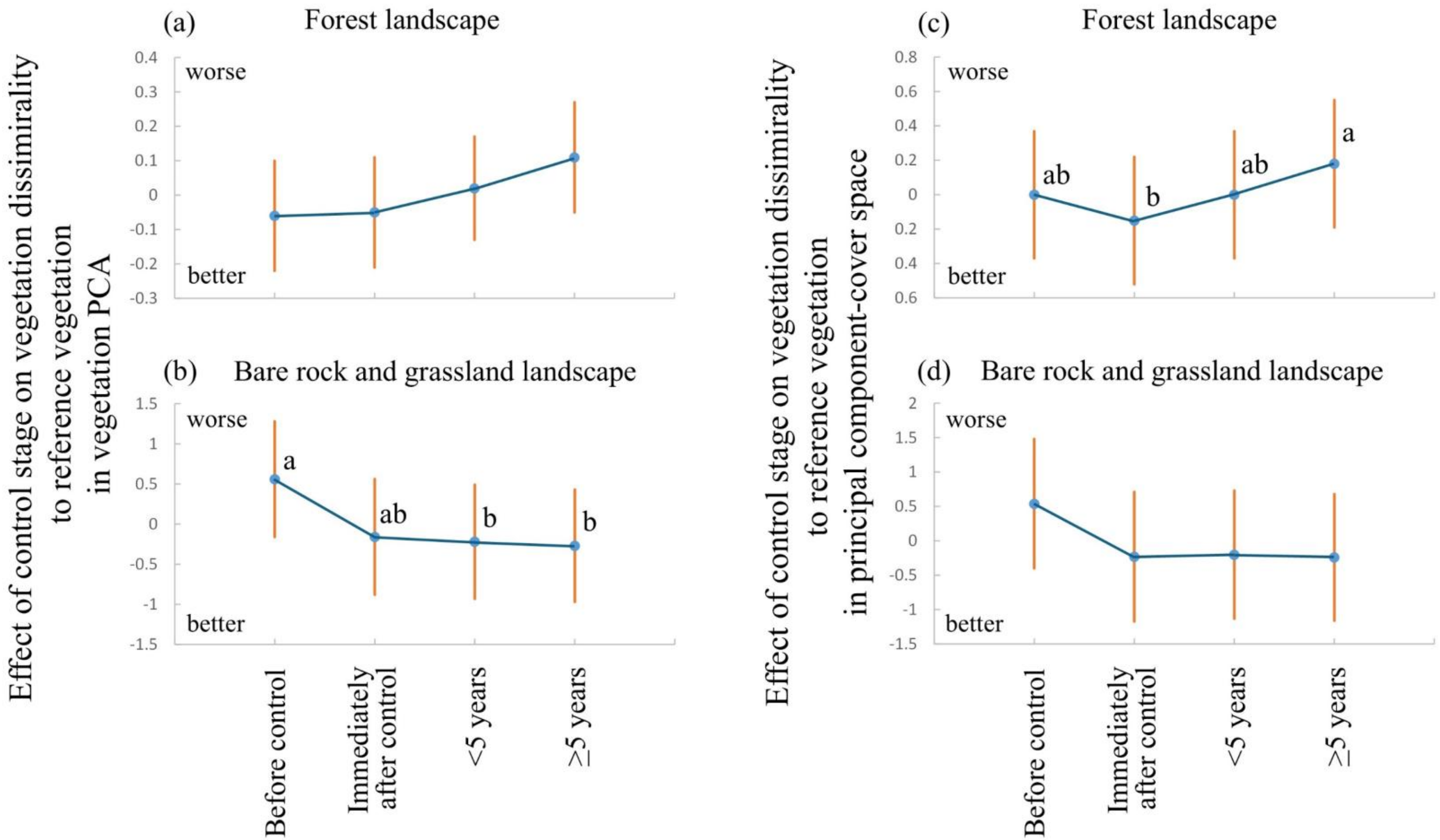

Forest landscape
Bare rock and grassland landscape
(a)
Native species
(b)
Alien species
(c)
Native species
(d)
Alien species
Effect of control stage on vegetation cover
better
worse
a
b
c
cd
bc
d
Reference vegetation
Before control
Immediately after control
<5 years
≥5 years

Fig. 5


(a) Forest landscape
(b) Bare rock and grassland landscape
(c) Forest landscape
(d) Bare rock and grassland landscape
worse
better
Effect of control stage on vegetation dissimilarity to reference vegetation in vegetation PCA
Effect of control stage on vegetation dissimilarity to reference vegetation in principal component-cover space
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
1.5
1
0.5
0
-0.5
-1
-1.5
0.8
0.6
0.4
0.2
0
0.2
0.4
0.6
2
1.5
1
0.5
0
-0.5
-1
-1.5
a
ab
b
b
ab
b
ab
a
Before control
Immediately after control
<5 years
≥5 years