





REVIEW

Not just for programmers: How GitHub can accelerate collaborative and reproducible research in ecology and evolution

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Abstract

1. Researchers in ecology and evolutionary biology are increasingly dependent on computational code to conduct research. Hence, the use of efficient methods to share, reproduce, and collaborate on code as well as document research is fundamental. GitHub is an online, cloud-based service that can help researchers track, organize, discuss, share, and collaborate on software and other materials related to research production, including data, code for analyses, and protocols. Despite these benefits, the use of GitHub in ecology and evolution is not widespread.
2. To help researchers in ecology and evolution adopt useful features from GitHub to improve their research workflows, we review 12 practical ways to use the platform.
3. We outline features ranging from low to high technical difficulty, including storing code, managing projects, coding collaboratively, conducting peer review, writing a manuscript, and using automated and continuous integration to streamline

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analyses. Given that members of a research team may have different technical skills and responsibilities, we describe how the optimal use of GitHub features may vary among members of a research collaboration.

4. As more ecologists and evolutionary biologists establish their workflows using GitHub, the field can continue to push the boundaries of collaborative, transparent, and open research.

KEYWORDS

collaboration, data management, ecoinformatics, GitHub, open science, project management, reproducible research, version control

1 | INTRODUCTION

Most scientists, including ecologists and evolutionary biologists, rely on computational tools for their research (Hannay et al., 2009). Researchers write and use software packages or write code to perform tasks ranging from data management, data analysis, and study replication, to the application and the development of tools for hypothesis testing. Maintaining code for scientific collaboration requires an efficient and well-documented workflow (Perkel, 2020). To facilitate this process, scientists have been adopting tools from information and systems technology, such as cloud-based services for documentation and version control (Perkel, 2016). These include Google Suite, Microsoft Suite, DropBox and GitHub. Within the spectrum of cloud-based services for collaboration, GitHub is uniquely positioned (Table 1) to benefit scientists because it is specifically designed to store, track changes, and enable collaboration on computer code—fundamental components of modern research. Albeit, many researchers lack exposure to adequate programming and coding practices and thus dedicate valuable time and effort to teach themselves research-facilitating tools. In this paper, we provide researchers in ecology and evolutionary biology (EEB) with practical workflows to use GitHub—the most used web-based platform for computational version control and collaboration—to facilitate their collaborative research and code management practices.

GitHub (<https://github.com>) provides a simple but powerful web interface that allows users to participate in projects by contributing, modifying and discussing existing code, reporting bugs, discovering code and data, and publishing new code. It stores files and directories in repositories, and keeps a chronological record of modifications (Bryan, 2018; see Box 1). GitHub also integrates several communication features, such as Github Issues, Github Discussions, Github Pages, which allows users to engage in discussions, to plan and collaborate on code, and publish information to a webpage (see Box 1). These features are an improvement over traditional practices of directly sharing files through email, other cloud-based services or physical storage units, which can become challenging and time-consuming in long-term and collaborative projects (Ram, 2013). By making it easier to integrate versioning, communication, collaboration with research code and data, Github helps facilitate open science practices in research projects (Perez-Riverol et al., 2016).

Git is the version control system that enables the collaborative tools available on GitHub. Git was initially developed as a fast, lightweight, and open-source system to allow software engineers to efficiently develop and collaborate on projects (Git-A Short History of Git, n.d.). Since its launch in 2005, Git has become the leading version control system in software development and in other disciplines that require collaboration and community contributions, such as in scientific research (Spinellis, 2012). To understand how GitHub keeps track of changes to files and folders, it is recommended to have knowledge of basic concepts of Git (such as commit, push, pull, and checkout; see Box 1). However, the GitHub web-based platform and its integrated development environments (such as GitHub Desktop) allow users to perform most repository and data management operations without using the command console, making these functionalities available even to users who are less familiar with software development.

Version control involves tracking the state of the files and directories which are stored in a “repository” (see Box 1). A typical workflow using Git and GitHub is to: (i) create a remote repository that is synchronized with files and directories stored locally; (ii) modify these files, either locally or remotely; (iii) frequently “commit” (or record) changes to these files (see Box 1) along with a description of modifications; (iv) synchronize commits with GitHub (see “push” and “pull” in Box 1) so that the repository on the web and the local repositories are up-to-date. The repository, which contains files, their modifications, and the description of their changes can then be accessed by chosen collaborators or, whenever applicable, the public, who can easily download and synchronize them to their own computers (see “clone” in Box 1). Commits act like snapshots, allowing users to view or even revert the state of the project to any previous commit. If the modified files are plain text, only the differences from the previous commit are recorded, allowing frequent commits without causing the size of the project to grow excessively. This provides a safe and less cluttered alternative to frequently making full copies of documents at different points in their evolution (e.g. analysis.R, analysis_v2.R, analysis_FINAL.R). While we do not focus on technical details about the use of Git and GitHub in this study, we recommend users explore available resources to become more familiar with version control features (see Blischak et al., 2016; Kalliamvakou et al., 2015; Perez-Riverol et al., 2016).

TABLE 1 A comparison of technologies commonly used for collaborating on research in Ecology and Evolutionary Biology. In the first column, we group platforms for collaboration into broad guilds. The second column lists the platform for collaboration. The remaining columns indicate whether the platform for collaboration includes certain features.

| Guild | Software | Version control | Cloud-storage backup | Passive collaboration | Active real-time collaboration | Does it provide a reasonably unrestricted free version? | Is it permanent (e.g. through a DOI)? | Storage limits | GitHub integration |
|--------------------------------------|------------------------|-----------------|----------------------|-----------------------|--------------------------------|--|--|--|--------------------|
| Multi-tool | GitHub | Yes | Yes | Yes | No | Broadly used free version. Advanced features are provided for free to students and education professionals | A DOI can only be obtained when integrating to other services that can mint a DOI (e.g. Zenodo, OSF) | 100 MB per file, 500 MB per private repository (2 GB for paid accounts), 100 GB for public repositories. Larger files (up to 2 GB) can be attached to releases | Not applicable |
| Multi-tool | Open Science Framework | Yes | Yes | Yes | Yes | Yes | Yes | 25 GB for private projects, up to 5 GB per file, plus partner add-ons, 50 GB for public projects | Yes |
| Long-term (public) data repositories | PANGAEA | Yes | Yes | Yes | No | Yes | Yes | 10 GB free | No |
| Long-term (public) data repositories | Zenodo | After published | After published | Yes | No | Yes | Yes | 50 GB per dataset | Yes |
| Long-term (public) data repositories | Dryad | After published | After published | Yes | No | No, however certain journals cover costs | Yes | 300 GB per publication | No |
| Long-term (public) data repositories | Figshare | Yes | Yes | Yes | No | Yes | Yes | 20 GB free, up to 5 TB | Yes |
| Temporary (personal) drive storage | Google Drive | Yes | Yes | Yes | Yes | Free version is restrictive | No | 15 GB free, up to 100 GB with Google One | Yes |
| Temporary (personal) drive storage | Box | Limited | Yes | Yes | Yes | No | No | Unlimited total size for subscription | Yes |
| Temporary (personal) drive storage | DropBox | Limited | Yes | Yes | Yes | Free version is restrictive | No | 2 GB free | Yes |

TABLE 1 (Continued)

| Guid | Software | Version control | Cloud-storage backup | Passive collaboration | Active real-time collaboration | Does it provide a reasonably unrestricted free version? | Is it permanent (e.g. through a DOI)? | Storage limits | GitHub integration |
|-------------------------------------|--------------------------------|-----------------|----------------------|-----------------------|--------------------------------|--|---------------------------------------|---|--------------------|
| Temporary (personal) drive storage | OneDrive and the Office Suite | Yes | Yes | Yes | Yes | Free version is restrictive | No | 5 GB free, up to 1 TB paid | Yes |
| Collaborative code and text editors | Overleaf (online latex editor) | Yes | Yes | Yes | Yes | Free version is restrictive. Only affiliated institutions (majority from the Global North) obtain premium access | No | 1 MB for individual LaTeX files, 50MB for individual files, unlimited project size | Yes |
| Collaborative code and text editors | Jupyter Notebook | Yes | Yes | Yes | With Colab | Yes | No | Via Binder: no hard limit, but suggests no files >100MB, can also store on GitHub or Google Colab | Yes |
| Collaborative code and text editors | HackMD | Yes | Yes | Yes | Yes | Free version is moderately restrictive | No | 3 documents free, private invitee limits | Yes |
| Collaborative code and text editors | Collaboratory | Yes | Yes | Yes | Yes | Free version is moderately unrestricted unless high computational resources are required | No | Colab's free of charge notebooks can run for at most 12 h. File storage is bounded to Google Drive's limitations. 12 GB GPU RAM | No |

BOX 1

Glossary

Repository: A repository (commonly shortened to “repo”) is a collection of files (e.g. a directory) tracked by Git. Repositories are managed by an owner and can be made either “public”, to be visible to all GitHub users, or “private”, to selected owner-specified users. Repositories can be either “local” and saved on an individual's computer or “remote” and stored on the cloud via GitHub's web platform.

Fork: A fork is a copy of a **repository** hosted on GitHub. If a repository is public, then anyone can make a fork. Even if they do not have access to **push** to the original repository, they can make a fork and edit it independently. Forks are linked to the original GitHub repository and “upstream” changes (i.e. those in the original repository) can be **merged** to keep the fork up-to-date with the original project. Changes made in the fork can be integrated into the original project via **pull requests**.

Clone: Cloning a **repository** is a way of making a local copy (i.e. on your computer) of a GitHub **repository**. If you have access to **push** to a **repository**, this can be a first step to contributing to a project.

Branch: Git workflow timelines or repositories are analogous to trees, with a main working project and diverging branches that are pointers to changes during the development process. A git branch is an alternative line of development for a project (repository). Branches allow users to add new features or modifications to the project without affecting the main part of the project. Development branches can be created at any point in time and work on each branch can continue independently. Branching is useful for testing out new ideas (both code and text) which may or may not eventually get integrated into the main branch of the project. Branches can also be used to isolate contributions of multiple contributors. Each person working on their own branch eliminates problems that may arise if conflicting edits are **pushed** to the same remote branch. Changes in a development branch can be **merged** into the main branch via **pull requests**. Branches can only be made by those who are given access to the project **repository**.

Commit: Commits are snapshots of the development of a project. In Git, versions of files and directories are uniquely identified as “commits”, allowing one to identify and track modifications line-by-line. Commits can include changes in multiple files and must include a brief commit message describing the changes made. A typical workflow is to make some related changes in files, add a commit message (e.g. “Generate and include results figure”), and after several commits **push** those commits to the remote (i.e., cloud-based) GitHub **repository**.

Push and pull: When **commits** are made in a project locally, they must be synced with the remote GitHub repository by **pushing** them. Changes on a GitHub repository can then be **pulled** to keep your local version of the project up to date with the remote.

Pull request: A pull request is a request for changes made on an individual's **branch** in the repository or in a user's **fork** to be merged to the repository. Pull requests contain a description of the changes alongside all code required for testing and review by other users prior to being merged into the repository.

Merge: Combining **commits** from two different branches together into one **branch**.

Release: At any point, a release can be made on GitHub to mark a significant milestone in the progression of a **repository**. While this GitHub feature is designed with releases of new versions of code in mind (e.g. v1.0.0), it can also be used to create a snapshot of a repository at significant stages like pre-print, submission, revision, and acceptance of an associated manuscript.

Community: A forum where GitHub users can ask for advice, offer solutions to questions, and share ideas (<https://github.community/>).

The use of GitHub has become increasingly popular in recent years due to the expansive GitHub user-community and numerous GitHub resources (Bryan, 2018; Happy Git with R, n.d.; Our Coding Club, n.d.; Perez-Riverol et al., 2016). Nevertheless, although multiple articles have encouraged researchers in ecology and evolution to adopt GitHub as part of their research process (Lowndes et al., 2017; Perkel, 2016), its use is still not widespread. Among many other factors, this may be because first-time users without formal training in information technology can face a steep learning curve, as GitHub and its features have been centred on software development (Leibzon, 2016). Furthermore,

there are few domain-specific resources providing tractable examples and practical guidance for researchers in EEB on how to use GitHub (but see Kim et al., 2022; Openscapes, n.d.; Our Coding Club, n.d.). Widespread adoption of GitHub for collaborative research tasks can ultimately enable EEB researchers to save time on creating novel processes for collaboration and focus more on their research (Briney et al., 2020). More importantly, expanding the availability of data and code management standards, of which GitHub is an increasingly important component, makes research more reproducible and collaborative (Alston & Rick, 2021; Gomes et al., 2022).

This paper is the result of an academic hackathon held during the 2021 conference for the Society for Open, Reliable, and Transparent Ecology and Evolutionary Biology (SORTEE, <https://www.sortee.org>). We convened around 30 researchers in EEB with varying levels of familiarity with the use of GitHub in research projects. The aim of the hackathon was to showcase and discuss how existing features of GitHub can contribute to documentation and collaboration in EEB research. During the event, we identified the need for formal discussions on how EEB researchers can benefit from GitHub and its features. Here, we outline 12 practical ways that EEB researchers can use GitHub features for more collaborative, transparent, and reproducible science. We also provide critical perspectives on features that could be improved and catered towards research development, drawing on examples from literature.

2 | TWELVE PRACTICAL WAYS GITHUB CAN ACCELERATE RESEARCH IN ECOLOGY AND EVOLUTION

2.1 | Storing and sharing research compendia

An EEB research compendium includes all computational materials related to research production, including data, code for analyses and protocols. Safely storing these files is essential to protect against accidental modifications or deletions. Many researchers begin using GitHub to backup their research compendium (Marwick et al., 2018) into a centralized, readily available remote server (see [Box 1](#)). This practice has the advantages of facilitating collaboration, integrating data and code archiving, allowing file versions to be accessed and restored, and further contributing to open science practices (Borghi & Van Gulick, 2022). Changes made to files in version-controlled repositories are accompanied by authored descriptions of modifications ([Box 1](#)). Later, the entire history of commits and their commit messages are viewable and can be audited similarly to physical laboratory notebooks (Ram, 2013). GitHub allows administrative control over who can view and modify repositories, and the process of cloning, forking and suggesting changes through pull requests (see [Box 1](#)) ensures code owners have full control over code and documents. Repositories can be changed from public to private, allowing data storage and management without sacrificing the privacy that may be necessary for certain compendia. With this, researchers can grant collaborators read and/or write access to files in private repositories to pursue pre-publication analyses or writing in privacy.

GitHub limits committed file sizes to 100Mb (megabytes) (About large files on GitHub, [n.d.](#)), which may require external file storage alternatives (such as local or cloud-hosting) for some parts of research compendia. However, users can still track versions of remotely or locally stored files in their repositories using Git Large File Storage (<https://git-lfs.github.com>).

2.2 | Project continuity

Projects in ecology and evolution often involve research professionals holding limited-term positions, such as graduate students, research assistants and post-doctoral fellows (Fehr et al., 2021). Without clear plans on project continuity, research code and data management upkeep tends to fall off as researchers move on to new projects or other institutions. Additionally, code and data can be difficult to access and recover when kept only on personal devices (Vines et al., 2014).

GitHub can facilitate project continuity in research by making code and data handover between users easier (Fehr et al., 2021; Ram, 2013). Through version control, the history of code and data from projects in ecology and evolution becomes accessible to future laboratory members and collaborators (Lowndes et al., 2017). Repositories and organizations can have designated data and code owners (or more appropriately, “data stewards”; see About code owners, [n.d.](#); Hampton et al., 2015), who can also change through time, allowing for the transition of code between research cohorts (see also “Organizing and managing teams”). Other project collaborators can contribute to repository design and development, and their active involvement can both aid authors ability to act as guarantors, and the clarity and reproducibility of the project for future users. In ([Figure 1](#)), we highlight several elements of recommended repository structure, and the various ways that contributors may interact with them.

Software compatibility during the analysis and reanalysis of project data can be ensured by storing information about software dependencies and their versions within the same project repository. With more advanced practices, one can remotely instal and execute scripts using specific versions of software within GitHub's project automation tools, GitHub Actions (see below).

In addition to projects, long-term management of laboratory materials (such as notebooks or experimental protocols) can also be done within GitHub, a practice that has been increasingly adopted across many fields (Perkel, 2016), including applied ecology (e.g. <https://scheuerell-lab.github.io/lab-book>), biogeography and global change biology (e.g. https://github.com/HuckleyLab/how_we_work), and microbial ecology (e.g. <https://github.com/CarBBAS/uqam-guide>).

2.3 | Project management

Modern research in ecology and evolution is highly collaborative, bringing together multidisciplinary teams from various institutions (Goring et al., 2014). On GitHub, collaborators can share feedback, brainstorm ideas, and troubleshoot problems ([Figure 1](#)). Project management can happen via three GitHub repository features: “Issues”, “Discussion” and “Projects” ([Box 1](#)). Github Issues allow for discrete tasks and sub-tasks to be identified, assigned to team members, and categorized with custom labels. Github Discussions serve as a message board for conversation. Finally, GitHub Projects

(a) Multi-faceted components allow for code writing, small data storage, manuscript writing, and project management to all be done in one place. CONTRIBUTING.md, LICENCE.md and README.md files allow new team members, or others wanting to use materials, to understand the project components and learn how they can engage with the project and existing team members.

(b) Issues, Pull Requests, Discussions and Projects allow team members to ask for feedback, suggest fixes, discuss related ideas, and keep track of all the moving parts of a project.

(c) All collaborators on a project can be a part of a single repository, with varying push privileges and responsibilities.

FIGURE 1 An overview of Git's core features. (a) Multi-faceted components allow for code writing, small data storage, manuscript writing, and project management to all be done in one place. CONTRIBUTING.md, LICENCE.md and README.md files allow new team members, or others wanting to use materials, to understand the project components and learn how they can engage with the project and existing team members. (b) Issues, Pull Requests, Discussions and Projects allow team members to ask for feedback, suggest fixes, discuss related ideas, and keep track of all the moving parts of a project. (c) All collaborators on a project can be a part of a single repository, with varying push privileges and responsibilities.

provides users with real-time tracking of project priorities and status (About Projects, n.d.). For instance, one can create a discussion on a project repository to decide which method to apply for biodiversity data analysis. Then, an issue can be created to establish steps and responsibilities including data formatting, statistical analyses, figure generation, and issue resolution. For example, sPlotOpen (Sabatini et al., 2021) manuscript repository contains issues and discussions tracking the development of the project (see https://github.com/fmsabatini/sPlotOpen_Manuscript/issues). Using GitHub for all project-related conversation and planning, rather than email or messaging tools, makes it easier to keep track of progress throughout the lifespan of a project. However, one can opt to receive new issues, discussions and responses as emails and can post replies by email as well. This allows for centralized communication for a team even when some members prefer to use email for communication. Unlike emails and messages which can get lost as more new tasks

arise, GitHub issues are intentionally closed by repository administrators hiding the issue from view (closed issues remain accessible but not immediately visible).

2.4 | Educational materials

GitHub supports a broad set of mechanisms for hosting educational materials. The entire process of running a course, workshop, or lecture, can all be done openly on GitHub including material development, web hosting, and delivery, and even submission and grading of assignments. While there are other purpose-built platforms for this, GitHub provides a free, open-source alternative.

Syllabi, presentations, and other course materials can be version-controlled, stored and managed in GitHub. While any file type for presentations and documents can be stored and tracked

in repositories, GitHub can directly render and display certain markup languages, such as HyperText Markup Language (HTML) and Markdown documents, making these file types especially useful for educational materials. Course content can then be delivered to the audience by sharing links of web-hosted GitHub Pages (see Hosting a Website), GitHub Repositories and/or GitHub Organizations. Finally, instructors can host and assign student work to be submitted collaboratively or individually as code and text files, and even build autograding tests using the GitHub Classroom tool (<https://classroom.github.com>).

Although time-consuming, adopting these features in classrooms can integrate the learning of version-control and GitHub practices with the learning of course contents, and thus boost students' feelings of self-efficacy and confidence (Trujillo & Tanner, 2014).

2.5 | Hosting a website

Personal or laboratory websites can improve the sharing of research findings, build online presence, and increase coordination of research efforts (Smaglik, 2007). Despite researchers in ecology and evolution generally lacking experience in building or hosting webpages, many tools have been developed to help this process. Static websites can now be easily built (using, for example Quarto [<https://quarto.org>], RMarkdown, Hugo [<https://gohugo.io>], GitHub Website templates [<https://github.com/topics/website-template>]), stored in a repository and be readily hosted by activating GitHub's Pages (<https://pages.github.com>) feature. Creating and hosting websites on GitHub Pages is more complex than out-of-the-box platforms (e.g. Wix, Weebly, Google Sites). However, free hosting, widely available template customization and versioning are strong advantages over alternatives.

2.6 | Archiving citable code and data

Government, funding agencies, and publishers exercise rigorous open-access data policies and mandates (Nugroho et al., 2015; Tenopir et al., 2020). However, code and data sharing may be met by individual reluctance, temporary embargoes, or partially prevented by privacy and confidentiality reasons (Figueiredo, 2017; Tenopir et al., 2015; Wicherts et al., 2011). Still, data deposition and ensuring its availability can amplify the outreach of published studies (Pronk et al., 2015), increase citation rates (Piwowar et al., 2007), and among many other reasons, enable the reproducibility and robustness of scientific advances (Baker, 2016; Mislan et al., 2016; "On Data Availability, Reproducibility and Reuse," Nature Cell Biology, 2017). While public repositories on GitHub make it easy to store and share data files, they are not considered long-term repositories for research materials. This is because GitHub, a for-profit company, does not have long-term data availability guarantees, allowing users to delete or make repositories private after publication. Also, GitHub does not issue Digital Object Identifiers (DOI) for content uploaded to their servers. DOIs are persistent and citable

unique alphanumeric identifiers assigned to digitally stored research materials. Because of this, scientists sharing code and data through GitHub are strongly encouraged to independently submit their research materials to long-term data archives (e.g. Zenodo, Figshare, Dryad, OSF (Crystal-Ornelas et al., 2021; Perez-Riverol et al., 2016; Perkel, 2016); Table 1). Some of these options (Zenodo, Figshare and OSF) integrate with GitHub, allowing project, code and data releases (Box 1) to be archived with versioned, citable DOIs. Linking GitHub repositories with a DOI helps research become findable, and properly cited and can ensure long-term stability (Hampton et al., 2015). This strategy has been increasingly adopted in numerous studies in ecology and evolution (e.g. the Zenodo repositories Hudgins, 2022; Harper et al., 2018; the Dryad and OSF repositories Braga et al., 2021; Braga, Kembel, & Peres-Neto, 2023).

An important aspect of making code and data citable and reusable is to add an appropriate licence to protect intellectual property. Code published without a licence is under exclusive copyright (by default), protecting it from copy, distribution and modifications. One may grant specific rights to their code for reuse by adding licensing files and specifications within GitHub repositories (Adding a license to a repository, n.d.). The Choose a License (<https://choosealicense.com/non-software/>) website offers further guidance on the licences available for research and creative products. For example, Creative Commons (CC; <https://creativecommons.org/licenses/>) licenses can specify that shared code is intended for a specific analysis. A CC BY 4.0 license specifies that any code (or other creative products) must be appropriately credited to its original author when distributed, adapted or reused.

2.7 | Collaborative and asynchronous code editing

GitHub can serve as a platform for everyone working with research (e.g. supervisors or advisors, graduate students, postdoctoral fellows, and collaborators) to share in-progress work, and flag specific challenges or questions for each other (Table 2). Periodic code, data and text reviews are useful for identifying errors early in the research process (Song et al., 2020), and informing further training and mentorship to fill gaps in skills. This is facilitated by a group of core features of Git and GitHub that allow contributors to discuss and simultaneously work on a project. For instance, users can clone and fork repositories (see Box 1), allowing for modifications to be done on a linked copy of a repository, which can then later be merged into the main project through pull requests. Collaborators can comment on specific lines of code and text or suggest changes, which can then be incorporated with the click of a button, greatly facilitating peer review. Explicit project organization and increased communication within pull requests, in GitHub Issues, or in GitHub Discussions can help with project development and with potential merge conflicts due to users simultaneously working on the same sections. Moreover, version control allows researchers to make changes in code or documents without worrying about irreparably modifying someone else's work (see the "Storing and sharing research compendia" section).

TABLE 2 A non-exhaustive collection of ideas for how various GitHub features could be utilized for a research project. Here we have categorized contributors/collaborators into five roles. A Project Manager owns the GitHub repository for a project, and leads the academic project (e.g. lead author of a manuscript). A co-author contributes to writing and other aspects of research, but may have limited or no experience with programming, git, and/or GitHub. A code contributor writes or edits analysis code for the project. A code reviewer could be a project collaborator or a peer reviewer who reviews project code. They are familiar with coding, but not necessarily with git or GitHub (but they are willing to learn). Finally, community members could be other researchers or non-researchers interested in reproducing results, re-using code or data, or communicating with researchers involved in the project. These roles are not mutually exclusive—a co-author could also be a code contributor and code reviewer, for example. For definitions of the GitHub features, see [Box 1](#).

| Role | GitHub repository | README | Issue | Discussion | Pull request | Fork | GitHub pages |
|------------------|--|-------------------------------------|---|--|--|--|--|
| Project manager | Set contributor permissions, share code of conduct | Project description, citation, DOIs | Assign tasks to collaborators | Discuss project directions and goals | Approve and incorporate edits to code and/or writing | Approve and incorporate edits to code and/or writing | Share up-to-date reports, figures, or draft manuscript |
| Co-author | Edit Markdown text or add files | | Propose changes involving code (e.g. analyses, figures) | Discuss proposed changes to manuscript | | | |
| Code contributor | | | Suggest code changes | | Contribute changes to code, initiate code review | | Contribute to project website |
| Code reviewer | Find all code related to a project | | Highlight specific lines of code and make suggestions | | Review or recommended changes in code | | |
| Community | | | Suggest additional features and report bugs | Ask questions about data and code | | Create a linked, editable copy of the repository | View project website |

By enabling more comprehensive remote collaboration, GitHub encourages the exchange of ideas among researchers at different institutions and in different countries, which can serve to improve the quality of the research itself by providing open access to data and code.

2.8 | Writing a manuscript

Beyond supporting collaborative code development, GitHub can be used for writing manuscripts. Writing a manuscript and storing its associated data and code in GitHub increases scientific reproducibility because text, code, and data can be found in one place. Although it may involve more initial time investment for setup, GitHub has many features that support a powerful collaborative workflow when writing manuscripts (Ram, 2013). Text documents stored and versioned in GitHub can be instantly displayed when written in Markdown, a lightweight markup language increasingly popular among scientists. When manuscripts are written in Markdown on GitHub, co-authors can contribute changes or suggest revisions to a manuscript in the same ways they would contribute changes or suggest revisions to code (see Collaborative and asynchronous code editing). Relevant literature or issues can be suggested using the Discussions and Issues features.

Incorporating GitHub into the process of writing a manuscript does not necessarily mean pivoting to an entirely new workflow. For instance, authors who prefer writing in LaTeX or Markdown can synchronize Overleaf (Using Git and GitHub, n.d.), HackMD (<https://hackmd.io>), and other platforms directly with a GitHub repository. Similar GitHub integrations are available for projects stored in Dropbox, Google Drive, among other popular tools familiar to many scientists and their collaborators (Table 1).

We wrote this manuscript using Manubot, a modifiable workflow implemented in GitHub to automatically render manuscripts and automate bibliographical tasks (Himmelstein et al., 2019). Manubot uses GitHub's automation workflow, GitHub Actions, to combine and convert individual Markdown files into a single LaTeX document, which can then be converted to a Word or PDF document, and displayed as a webpage. Citations and bibliographic references are automatically managed with citable persistent identifiers (e.g. DOI, PubMed ID, ISBN, URL). The resulting manuscript can be rendered with document templates and citation style language formatting to meet journal formatting requirements. Every change made to the manuscript triggers its rendering, so that updates are readily displayed and made publicly available. Additional GitHub Actions can be integrated with Manubot, such as ones creating figures or generating tables (e.g. <https://github.com/SORTEE-Github-Hackathon/manuscript/tree/main/github/workflows>).

2.9 | Peer review

Peer review is the standard process for assessing whether research done in ecology and evolution should be published in a scientific journal. GitHub provides an open and transparent platform that can

be used for either directly providing feedback on research products or addressing changes recommended by reviewers. GitHub Issues can be used to organize and discuss reviewer suggestions and to assign them to co-authors (e.g. <https://github.com/SORTEE-Github-Hackathon/manuscript/issues?q=label%3A%22Reviewer+Comment%22>). When reviewer comments are posted as separate issues, authors can comment on the issues to discuss possible changes and assign co-authors who will address the issue. Co-authors can then integrate their edits and responses to reviewers using pull requests, which can be directly linked to the issues they address.

GitHub can also assist reviewers during the peer review process. If the code associated with a manuscript is made available at the time of submission (e.g. as a link to a GitHub repository within the Data Availability Statement), peer reviewers may be able to offer more comprehensive suggestions on the code and written materials, potentially recognizing errors before publication. Certain journals or software development communities require submitted work or research code to be hosted on GitHub and their review processes make use of GitHub Issues (e.g. rOpenSci <https://ropensci.org/software-review/>, Journal of Open Source Software <https://joss.readthedocs.io/en/latest/submitting.html>).

2.10 | Open science discussion

Scientific publications often omit part of their intellectual and computational workflows, including the treatment of raw data and analytical steps (e.g. model assumption testing). Publishing data and reproducible workflows along with manuscripts can provide readers with all details about analytical steps and enable reproducing research experiments and results (Culina et al., 2020). In addition to storing data and code, GitHub repositories can provide a time-stamped (version controlled) preregistration of research plans and hypotheses.

Conventional research practices typically separate tasks among collaborators (i.e. data entry, analysis, writing). It is common that co-authors discuss, but do not actively verify, edit or execute research tasks that are not their main responsibility. GitHub can serve as a tool for open and tractable research development. Collaborators can directly interact with code and data, inspect for errors and potentially identify scientific misconduct prior to manuscript submission (e.g. Kozlov, 2022; Viglione, 2020; <https://ecologyforthemasses.com/2020/02/04/pruittdata-and-the-ethics-of-data-in-science>). Collaborators and readers are better positioned to discover erroneous or questionable findings if they have complete and transparent access to projects.

This transparency can be extended beyond co-authors to the entire scientific community and to the public. Supplying code for novel or currently used methods reduces barriers to knowledge, improving the ability of others to build on existing work. This practice results in greater proliferation and accessibility for a broader audience. Projects can make use of GitHub Discussions (<https://docs.github.com/en/discussions>) to communicate among

repository members (collaborators) and to engage with other scientists and the general public. Moreover, researchers can also use the GitHub Community (<https://github.community/>) forum to share expertise or request help from others on their analyses and ideas (Table 2).

The desire or need for privacy during the developmental stages of a manuscript or of a larger research project is common in EEB, and this is often perceived as a major barrier to doing science openly. Because GitHub repositories can be made private or public at any time, there is no need to choose privacy over open science or vice-versa. Repositories can be kept private until their contents are ready to be shared publicly, as might occur when a research article is published or when an embargo is lifted.

2.11 | Automation

Automation has the strong potential to expand the scale and pace of research in ecology and evolution (Keitt & Abelson, 2021). Automation frameworks can streamline many stages of the scientific process, including data collection and data validation (e.g. Micheletti et al., 2021; Yenni et al., 2019), data analysis (e.g. Beaulieu-Jones & Greene, 2017), unit testing of research code (e.g. Sarma et al., 2016), archiving and deployment of data, code and reports (e.g. this manuscript, White et al., 2018), and the interpretation, integration and usage of data and software across different sources (see Pasquier et al., 2017). In this context, small modifications to code and data can be frequently committed and automatically tested, as in continuous integration and continuous deployment practices (Meyer, 2014). This allows for early detection and correction of errors, potentially improving confidence in scientific development by minimizing software errors (see Soergel, 2015). In addition to increasing scientific rigour and confidence in ecological software (Scheller et al., 2010), automation can help advance more rapidly sharing ecological data and making sure the data are high quality (Dietze et al., 2018). Integrating automation workflows has been highly encouraged in areas of EEB, including predictive ecology (McIntire et al., 2022), long-term ecological studies (Ernest et al., 2018; Yenni et al., 2019), and management of species at risk information (Naujokaitis-Lewis et al., 2022).

Automation can be integrated into GitHub repositories through the GitHub Actions feature (Features • GitHub Actions, n.d.), or through alternative automation systems (e.g. Circle CI, Continuous Integration and Delivery, n.d.; Home – Travis-CI, 2022). Users can set up workflows associated with their repositories that are triggered by events (e.g. push, pull request or at specified times) for remote servers to perform user-specified steps and actions. These actions are highly configurable and have numerous applications, such as automatically running analyses and creating figures when data or code are updated, incorporating changes to websites or applications, testing modifications to software (e.g. R or Python libraries). Action workflows can be found in GitHub's Marketplace (<https://github.com/marketplace?type=actions>) or, alternatively, in open user repositories.

2.12 | Organizing and managing teams

GitHub Organizations are shared virtual spaces that allow teams to work in different repositories, while remaining tied together under a larger group, such as a laboratory, department, or project involving several teams. Organizations allow larger projects with many steps or moving parts to be constrained to one virtual space, where outputs and sub-projects can be easily accessed and located without relying on individuals. Because the repositories are grouped, members can reference and contribute to each other's work without necessarily being part of the same repository, broadening the accessibility and longevity of code and writing contributions.

Contributors can be assembled into teams within an organization, which allows administrators to assign roles, tasks, and repository modification permissions to organization members. Whereas access to repositories is usually assigned to individual contributors, organizations facilitate the management of access permissions by allowing teams to be granted access to specific repositories. This ensures repositories with sensitive information remain as restricted as needed, while others stay open and accessible to selected member groups. The organization structure also allows for issue tracking and discussions related to research content and progress.

As an example, GitHub Organizations are particularly well-suited to host documents and projects within a laboratory, such as research compendia, codes of conduct, protocols, training documents and other relevant documents that evolve collaboratively over time. In this way, teams have full ownership of repositories within an organization, while ensuring that these materials stay accessible to the laboratory after people have moved on or when locally-stored data are lost. This application extends to research centres, which may include several distinct projects that remain linked to institutions [e.g. the German Centre for Integrative Biodiversity Research (iDiv, <https://github.com/idiv-biodiversity>)]. The team organizing the hackathon which inspired this article used a GitHub Organization (SORTEE-Github-Hackathon, <https://github.com/SORTEE-Github-Hackathon>) to centralize the project development, from meeting notes to, ultimately, this manuscript. Organizations are also convenient for hosting learning materials, including lectures or workshops, such as the Québec Centre for Biodiversity Science R Workshop Series (QCBSRworkshops, <https://github.com/QCBSRworkshops>) or the University of Edinburgh's Coding Club (Coding Club, <https://github.com/ourcodingclub>), which may be continuously updated by an ever-evolving group of contributors.

3 | DISCUSSION

3.1 | The promise of GitHub for ecology and evolutionary biology researchers

Many researchers outside of software development have been encouraged to use GitHub for their collaborative research (Anbaroglu, 2021; Crystal-Ornelas et al., 2021; Perkel, 2016). This is largely due to the

rise of open science and the growing computational and data needs of ecology and evolutionary biology. While tools like Google Suite and DropBox enable rapid sharing and collaboration of some research documents, GitHub brings together features that directly integrate open science practices. These include linking data, code and findings to public discussions, tracking edits to files for review, and managing complex research projects with many collaborators and goals. Until now, resources and practical guidance on using GitHub within the EEB community have been scattered across blog posts, written and video tutorials (Box 2). These resources have been useful for learning to use GitHub in our own research, as ecologists and evolutionary biologists. We expect that situating the main uses of GitHub in EEB alongside examples in this paper will be useful to the EEB community.

The 12 use cases we described here can leverage GitHub to enable more transparent and collaborative research in ecology and evolution

(Figure 2). Most of these uses can be quickly integrated into researchers' practices, such as storing data, creating virtual notebooks, and making code citable. Making stored data and code citable usually involves creating a repository on GitHub, pushing code and data, and then integrating a DOI minting service to the repository (e.g. with Zenodo or OSF; see below). On the other hand, some cases we described here, including course material development, web hosting, and automation, require more effort and time, but have the potential to make ecology and evolution research more open, accessible, and collaborative. If researchers wish to manage full research projects or laboratories on GitHub, they should consider how to delegate tasks, such as reviewing pull requests or creating issues. For example, collaboratively authoring a paper using GitHub, as we have done here, involves a learning curve for co-authors less familiar with the intricacies of GitHub, requires overhead to set up automation frameworks through GitHub Actions,

BOX 2

Ten tips for getting started in GitHub

- 1. Check for existing solutions to your problem.** The GitHub Help webpage (<https://docs.github.com/en>) contains extensive and detailed documents with helpful screenshots. It is a good starting point for handling an issue, and has troubleshooting tips for specific problems. Alternatively, consider Tweeting your issue. There is a large community of GitHub users around the world who have likely faced analogous problems and may be able to provide quick solutions. Third, try to follow blogs (e.g. <https://github.blog>), Twitter accounts or YouTube channels that regularly post practical solutions about the most widely-used web platform for common GitHub issues.
- 2. Consider taking free courses,** such as those from Software Carpentry (Munk et al., 2019), and sharing them with your lab members or colleagues.
- 3. Take advantage of GitHub as an asynchronous working tool for team-based projects.** See the repository for this paper (<https://github.com/SORTEE-Github-Hackathon/manuscript>) as an example of a collaboratively authored manuscript that used the GitHub Discussions, Issues, Pages, and Actions features.
- 4. Use the interactive courses from the GitHub Skills page** (<https://skills.github.com/>), which allow you to learn GitHub basics through short projects and tasks with step-by-step guides.
- 5. Learn markdown and use cheatsheets** (e.g. <http://markdownguide.org/basic-syntax>) so you can write clear metadata README files for your repositories.
- 6. Consult online resources.** The Jenny Bryan Universe of GitHub material, for example, provides a thorough and accessible introduction to a multitude of research-related uses for GitHub and includes a book (Hester & the STAT 545 TAs, n.d.), statistics course (Bryan & TAs, n.d.) and academic article (Bryan, 2018).
- 7. Do not be afraid of trial-and-error.** One of the best ways to learn GitHub is the "trial-and-error" method. Learning from your own mistakes can be a valuable way to master your GitHub abilities. In any case, if you make mistakes, GitHub allows you to revert any steps that you desire via version controlling.
- 8. If you are an educator, include lectures on reproducibility and tools for creating reproducible workflows in the curricula.** Some graduate programs include coursework on course R Markdown and GitHub. Getting students started with these tools earlier will prevent the resistance that comes from working with a less reproducible workflow for a longer period of time (see example https://github.com/rmcelreath/stat_rethinking_2022).
- 9. Try to begin committing with graphical user interfaces (GUI) instead of command line interfaces (CLI).** Examples of GUI are the GitHub Desktop (<https://desktop.github.com>), git-gui (<https://git-scm.com/docs/git-gui>), RStudio (<https://www.rstudio.com>), Visual Studio Code (<https://code.visualstudio.com>), Atom (<https://atom.io>), GitKraken (<https://www.gitkraken.com>).
- 10. Get help deciphering GitHub Notifications.** Try using tools like Octobox (<https://octobox.io>) to disentangle and manage multiple notifications from distinct GitHub projects.

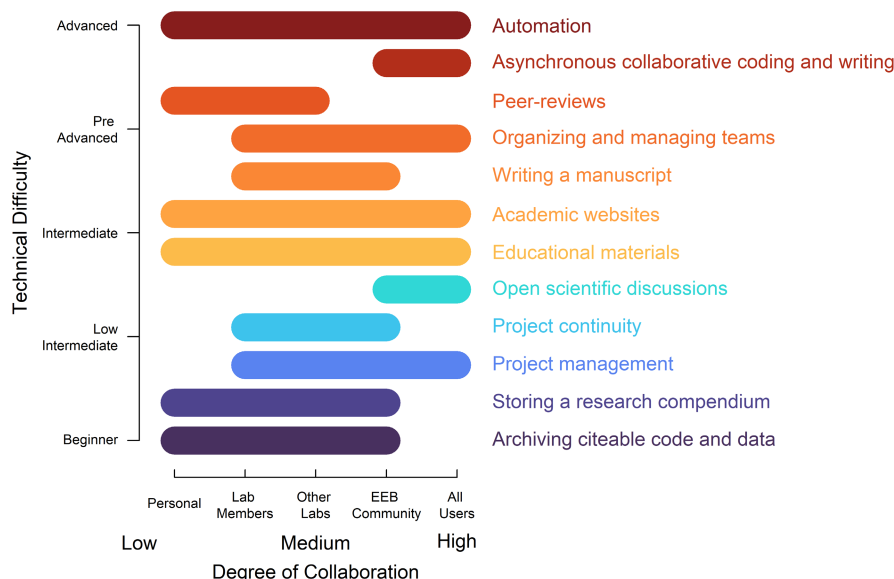


FIGURE 2 A summary of ways GitHub can be used showing technical difficulty and degree of collaboration for each. Activities higher on the vertical axis require usage knowledge of more GitHub features than activities lower on the axis. On the horizontal axis, each activity spans a region representing who is potentially involved with or benefits from each activity. For example, storing data and code mainly benefits individual researchers or members of a laboratory while making data and code citable and reproducible benefit other labs and the larger community as well. Independently of one's knowledge of GitHub features, there are ways to use GitHub that allow tapping onto one of the strongest benefits of the platform: facilitating and enhancing collaboration. For information on the methods and the data used to create this figure, see Appendix S1.1, Appendix S1.2, and Tables S1.1 and S1.2.

and especially, the commitment from all co-authors to use GitHub when modifying and reviewing the text. Despite the potential applications of GitHub to EEB research, we acknowledge that researchers might still look to other platforms for research collaboration.

3.2 | Other platforms for collaboration

Despite its strong collaborative potential, we describe two use cases where GitHub falls short of highly collaborative work.

First, real-time document editing is still best performed on other platforms, such as cloud-stored documents from Microsoft Word, Google Docs and HackMD (<https://hackmd.io/>). Second, operations that are dependent on software requiring graphical user interfaces might not be easily achievable in GitHub, such as designing and manipulating figures or tables. While creating tables and figures can be done through code, users may choose other software to collaboratively brainstorm figures and tables, like Google Slides or Google Sheets (but see GitHub Discussions).

3.3 | Why aren't more EEB researchers using GitHub?

Although GitHub has been available as a platform for more than a decade, its uptake among EEB researchers, especially as a tool for collaboration, has been slow. Here, we discuss five potential barriers to GitHub use in EEB:

First, there may be hesitation to independently adopt and learn a new tool. Institutional encouragement and instructional resources focused on researchers in ecology and evolution may be limited. Additionally, with the availability of software licences for tools like Google Suite or Microsoft Office, researchers may be reluctant to spend valuable time learning another tool. When GitHub is taught within an EEB context, it usually accompanies coursework in topics such as statistical programming. This can be difficult for those who lack programming experience, as they must learn Git alongside scripting languages, statistical theory, and file system navigation. Instructors may also confuse the expected digital literacy of students with computational fluency, despite modern technology abstracting concepts through search optimization and user-friendly integrated development environments (IDEs) or 'point-and-click' user interfaces.

Second, while EEB researchers individually use GitHub, collaborative use may lag due to researchers traditionally dividing labor within projects. Despite broad utility, GitHub remains a tool predominantly used by computer scientists and software developers. EEB researchers may take the view that GitHub is a platform that only needs to be used by individuals writing code, and may silo those aspects of projects to a single individual. These assumptions may obscure the utility of GitHub for tasks other than traditional data analysis and code development. However, we emphasize that there are opportunities for collaboration using GitHub by researchers of all skill levels or time constraints (Table 2). For example, project stakeholders can provide a list of use-cases or highlight important conceptual components of a project using GitHub Issues or Discussions features.

A third barrier to the use of GitHub may come from general reluctance to share data and code publicly, or technical and logistical issues (Gomes et al., 2022). GitHub is, by default, a public and open platform, which may add additional pressure to students and scientists learning to use it. Moreover, additional tools may be needed to fully integrate project files and GitHub repositories (e.g. Connect GitHub to a Project-OSF Support, n.d.). Other scientists may simply lack the time or incentives to document and version control their code if the code is unlikely to be reused beyond their analysis. However, we (and others, e.g. Gomes et al., 2022) argue that for open science and collaboration to be successful, code owners should document, and version control their code, despite uncertainty about future use.

A fourth additional barrier to EEB researchers is the lack language-specific resources for non-English speaking researchers working in ecology and evolution. Language is a well-known obstacle to international collaborative research progress and to widespread scientific knowledge (see Khelifa et al., 2022). Non-English speaking EEB researchers can potentially miss opportunities to fully integrate version control, reproducibility, and other benefits of GitHub without language-inclusive contents.

Fifth and lastly, when projects require a high degree of collaboration, they may need to pay for certain GitHub features, such as branch protections, multiple reviewers of pull requests and time in its automation tools. Fortunately, GitHub offers education packs (<https://education.github.com/>) to students and academics, which extend some paid features to the free plan. However, the acquisition of GitHub by Microsoft has raised concerns over the future of free plans, causing several biodiversity data managers to shift to alternative Open Source Git services, such as Bitbucket and GitLab.

4 | CONCLUSION

We provide 12 practical ways that ecologists and evolutionary biologists can use GitHub to improve their research workflow, make it more open, reproducible and transparent. We provide definitions (Box 1) and types of users (Figure 1) to help researchers identify and prioritize the skills and tools to learn and apply. We highlight tools providing high collaborative potential (e.g. open science discussion, collaborative code editing) to more individual focused (e.g. storing code and data, building a website). We argue that the tools readily available in GitHub have the potential to make ecology and evolution more open, reproducible and transparent. With this comprehensive review of how EEB researchers can use GitHub, we encourage researchers at any career stage to adopt GitHub as a platform for sharing and collaboration.

AUTHOR CONTRIBUTIONS

We indicate author contributions using the CRediT Taxonomy.

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CONFLICT OF INTEREST STATEMENT

On July 15, 2022, RCO was offered a position to work at GitHub and became an employee on August 23, 2022. Initial discussion of publishing this manuscript began in July 2021 and all work on the manuscript prior to the first revision was done while RCO was an employee at Lawrence Berkeley National Laboratory. The authors declare that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14108>.

DATA AVAILABILITY STATEMENT

The preprint and the entire source code containing the manuscript and author contributions is available in the Open Science Framework repository (accessible at <https://osf.io/bypfm/>; Braga et al., 2023) and GitHub repository (accessible at <https://github.com/SORTEE-Github-Hackathon/manuscript>) for this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1.1. Computing indices of technical difficulty and degree of collaboration.

Appendix S1.2. Annotated code and prose allowing the representation of indices of technical difficulty and degree of collaboration.

Table S1.1. Classification of depress of collaboration attributed to the use cases for GitHub in research in the field of ecology and evolutionary biology.

Table S1.2. Indices of technical difficulty and degree of collaboration for each GitHub use case. The first column lists the GitHub use cases that were addressed in the main text. Indices were assessed collaboratively following the steps in Appendix S1.1.

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